XIX. *Further Observations on the Organization of the Fossil Plants of the Coal-Measures.*—Part I. *Calamites, Calamostachys, and Sphenophyllum.*

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[Plates 72–86.]

PRELIMINARY NOTE BY W. C. WILLIAMSON.

A few words in explanation of the origin of this new enquiry may be desirable. During the investigations into the organization of the fossil carboniferous plants upon which I have been engaged for more than forty years, I have brought to light a number of structural features different from any discoverable amongst allied plants living at the present day. Though morphological truth was the main object of my researches, it was impossible wholly to exclude thoughts respecting the modes of growth by which these structural combinations have been produced. Many such suggestions are scattered through my numerous memoirs; some of them I believe to be true; others are fairly open to such doubts as have been expressed by my friend, Graf zu Solms, and others.

My morphological enquiries seem to have reached a stage that makes a more minutely careful examination of these questions of development and growth desirable; but before specially undertaking this, I saw clearly the extreme importance of doing so in combination with some younger colleague whose familiarity with the details of the physiology of living plants was greater than my own. Under these circumstances I have secured the co-operation of Dr. D. H. Scott, and the present paper embodies the results of our united investigations. The work has been carried out in the Jodrell Laboratory of the Royal Gardens, Kew. W. C. W.

I. CALAMITES.*

Introduction.

The fossil stems which we are about to consider, and which we include, in conformity

* References to the extensive previous literature of our subject will be found scattered through the series of memoirs, by W. C. Williamson, in the 'Philosophical Transactions of the Royal Society' (1871–1893). A full summary of our knowledge, up to 1887, is given by Count Solms-Laubach in his

with the usage of most English and German palæobotanists, under the generic name of *Calamites*, are characterized anatomically by the following features :

1. The axis is traversed by a well defined central cylinder, consisting of a large pith (which became fistular in all but the smallest specimens), and of a ring of distinct, collateral vascular bundles, separated from one another by broad radial bands of interfascicular tissue, or primary medullary rays (see Plate 72, photographs 1, 2, and 3 ; Plate 77, figs. 1, 2, and 3). Each vascular bundle has an intercellular space, or canal, on its inner side, and from the outer margin of this canal the radial series of xylem-elements extend.

The bundles run parallel to one another, without anastomosis, through the internode. At each node they turn outward, taking an almost horizontal course. The out-going bundles are all situated at the same level, forming a whorl. There can be no doubt from their position and course that they were leaf-trace bundles, supplying a whorl of leaves (see Plate 72, photographs 5 and 6 ; Plates 77 and 78, figs. 6, 7, 8, 11). As all the bundles of a whorl are alike, and they are equidistant one from another, there is a strong presumption that each leaf received a single bundle only. This presumption is fully confirmed by all that we know, from other sources, of the foliage of *Calamites*.*

The course of the vascular bundles in some cases follows the well-known simple type characteristic of *Equisetum*, those of successive internodes alternating regularly with each other. Considerable deviations, however, from this type are met with, and will be considered below.

2. The central cylinder is surrounded by a cortex, only preserved in comparatively few specimens (see Plate 72, photographs 1, 2, 3 ; Plate 77, figs. 1, 2, 3 ; Plate 78, fig. 12 ; Plate 79, fig. 18). In some cases the cortex is but little differentiated, showing only a few thick-walled elements among the parenchyma, while in others it consists of two distinct zones, of which the outer is more sclerotic than the inner.

3. The *branches* are placed immediately above the node, each branch being so situated, in almost all cases, that its centre-line lies midway between two of the leaf-traces which pass out at that node (see Plate 72, photographs 5 and 6, and Plate 80, fig. 21). The number of branches developed is very variable, but seems to be always much less than that of the leaf-traces. Although placed above the node, the wood of the branch is directly continuous with that of the bundles below it.

4. Neither leaves nor roots have been found, so far, in connection with the specimens investigated by us, in which the internal structure is preserved. As regards the roots, however, we have now some important information from other sources, which we shall consider at a later stage.

"Introduction to Fossil Botany" (English Translation, 1891, chapters 13 and 14), where the literature is very completely cited. Only the most necessary references are given in the present paper.

* See, for example, WEISS, "Steinkohlen-Calamarien," vol. 2, p. 26, plate 1; RENAULT, "Cours de Botanique fossile," vol. 2, plate 17.

5. The above general characters are common to all the stems observed. The specimens, however, present great differences among themselves, which are due (1) to the *order* of the branch in question, or to the *part* of the branch from which the specimen is derived; (2) to age; and (3) to specific distinctions. The differences under the first two heads can be readily distinguished from one another with proper care. It is, however, we believe, as a rule, impossible to distinguish between branches of different orders belonging to the same species and those of different species, though in special cases, as in the form originally described as *Calamopitus*, the specific distinction is evident.* The same difficulty would exist in the case of *Equisetum* if we had to depend on isolated fragments of branches for our anatomical knowledge.

6. Variations in structure, due to the *part* of the branch from which the section is cut, are as follows:—

a. In the size of the pith and consequently of the primary central cylinder (see Plate 73, photographs 7, 8, and 9);

b. In the number of the vascular bundles;

c. In the presence or absence of the canals accompanying the bundles.

a. The size of the pith, in most if not in all cases, is at a minimum at the base of the branch, and increases rapidly upwards, until its approximate maximum is attained, after which it remains nearly constant.

b. In like manner the number of vascular bundles is at a minimum at the base of the branch, and increases in the ascending direction in successive internodes, until a maximum is reached, when it remains approximately constant.

c. The canals accompanying the bundles are absent from the base of the branch, but are otherwise almost always present in the internodes.

The evidence on which these conclusions are founded will be fully given below.

7. Variations known to be due to the *order* of the branch are: (*a*) in the size of the pith† and primary cylinder, and (*b*) in the number of the vascular bundles. It is probable that the solid or fistular character of the pith may also vary with the order of the branch, as well as with age, as is the case in many species of *Equisetum*.

8. Differences in the relative width of the bundles and primary medullary rays, in the structure of the rays, in the size of the canals, and in many other points, may either be of specific value, or be due to the order of the branch, or to mere individual variations.

9. Differences due to *age* consist (*a*) in the degree of preservation of the pith. The presence of a broad zone of persistent pith within the ring of bundles (see Plate 72,

* WILLIAMSON, "Organization of the Fossil Plants of the Coal-Measures," Part I., 'Phil. Trans.,' 1871, p. 488; 'Memoirs of the Literary and Philosophical Society of Manchester,' ser. 3, vol. 4, 1869.

† These variations are enormous in degree. The diameter of the pith in the specimen figured in Plate 77, fig. 1, is at most 0·3 millim. BRONGNIART describes his *Calamites gigas*, a medullary cast, as "*diametro pedem subæquante*." The ratio is about as 1 : 1000.

photograph 2; Plate 77, fig. 3, &c.) may, however, characterize certain branches, or even, perhaps, certain species.

(*b*) In the secondary growth of the vascular cylinder. In every stem of the types examined by us secondary thickening took place; only the very smallest twigs are destitute of it. So far as the evidence before us shows, there is not the slightest reason to believe in the existence of any *Calamite* which did not form a secondary zone of wood. Its formation has been observed at every stage. The radial arrangement of the elements is exceptionally clear as compared with most recent plants which have secondary growth. The phloëm and cambium are rarely preserved, but, as we shall see, they can be demonstrated in favourable cases.

(*c*) In the secondary growth of the cortex. It attained, in some old stems, a thickness even greater than that of the wood, and its increase was accompanied by an extensive development of periderm. To this subject we shall return.

There can be no doubt as to the specimens in question forming a perfectly natural group. With the exception of the *Calamopitus* type, and of *Calamodendron*, which latter we have not dealt with in this paper, all the forms examined might even have belonged to a single species, though it is much more probable that several allied species are included.

There is, further, no doubt that the specimens showing structure, with which we are more particularly concerned at present, belong to the same plants as the macroscopic specimens long known under the name of *Calamites*. The proof that the common form of preservation of these fossils represents merely the cast of the hollow pith, has been sufficiently enforced in previous memoirs.* Specimens, such as one in the WILLIAMSON collection, in which a cast of the pith is still partly enclosed by the well-preserved cylinder of wood, show quite clearly that the furrows on the surface of the cast correspond to the inner edges of the vascular bundles, while the ridges of the cast fit into the spaces left by the softer tissue of the broad medullary rays. Medullary casts from the base of branches, of which several are figured, agree perfectly with the form of the pith, as shown in specimens of the same parts, with structure perfectly preserved (see Plate 79, fig. 20; Plate 80, fig. 22; Plate 73, photographs 7, 8, and 9). In cases of doubt the medullary casts can be identified by their having a constriction at each node, while the opposite condition is conspicuous where the wood and cortex are present. (Compare the figures of casts in Plate 86 with the photograph 4, Plate 72; and with "Organization," Part XIV., figs. 5 and 6, 'Phil. Trans.,' 1888, vol. 179, B). The cortex presents no superficial ridges and furrows.

We may assume, then, that we are dealing with the histological structure of the same plants which have so long been known under the name of *Calamites*, of which the medullary casts are the most familiar form of preservation. The commonest type

* See "Organization," Part I., 'Phil. Trans.,' 1871, and Part IX., 'Phil. Trans.,' 1878, Plate 2. See also STUR, "Zur Morphologie der Calamarien," 'Sitzber. d. k. Akad. der Wiss. z. Wien., Math.-naturwiss. Classe,' Bd. 83, Abth. 1, Heft. V., 1881. SOLMS, 'Fossil Botany,' p. 301.

of these fossils in the English Coal-Measures is that of the so-called *Arthropitys*, GÖPP. As this genus was only separated from *Calamites* on account of its secondary zone of wood, which we now know to have been common to the whole group,* we shall retain the older generic name. The question, so keenly discussed since the time of BRONGNIART, as to the Cryptogamic or Phanerogamic nature of these remains, seems now to be definitely decided in favour of the former alternative.† As regards the vegetative organs, the presumption, derived from the occurrence and character of the secondary formations, seemed at first entirely in favour of Phanerogamic affinities, and we cannot wonder at the view so long held by BRONGNIART and many botanists of his school. Only a consideration of the whole body of evidence, both from recent and fossil plants, has decisively turned the scale the other way.

Among the Cryptogams the affinities of *Calamites* have always been sought in the neighbourhood of the Equisetaceæ. In considering the vegetative organs, then, the most interesting question is whether the *primary structure* shows a sufficiently close agreement with that of *Equisetum* to establish any presumption of relationship. The most obvious resemblances, which attracted the attention of the earlier palæobotanists, have turned out to be fallacious. Thus we now know that the supposed *Equisetum*-like ribbed stem is no ribbed stem at all, but merely a cast of the pith-cavity. The external surface of the larger specimens could not possibly have shown ribs like those of *Equisetum*, for in the latter genus these ribs represent the course of the vascular bundles, and these are overlaid in the older *Calamites* by an immense zone of secondary wood and cortex.‡

The points of vegetative structure on which stress may fairly be laid, for purposes of comparison with *Equisetum*, are the following :—

1. The arrangement, and relative position of leaves, branches, and adventitious roots.
2. The course of the vascular bundles.
3. Their orientation, and the order of development of their elements.
4. The details of histological structure.

The points under the first category are of manifest morphological importance; the others are each, by themselves, of secondary value, and only a strong resemblance in the *sum* of such characters could weigh for much in estimating affinities.

* *Cf.* GRAND'EURY, "Calamariées—Arthropitus et Calamodendron," 'Comptes Rendus,' 1889, vol. 108, p. 1086; also 'Flore Carbonifère du Gard,' 1890.

† We believe that M. RENAULT is now the only author who still attributes Phanerogamic fructifications to some of the Calamarieæ. See his "Étude sur le Terrain Houillier de Commentry," livre 2, 'Flore Fossile,' Part II.

‡ The shorter-lived branches no doubt had a comparatively thin secondary zone, and these, in the fossil state, may appear to show superficial markings. It has already been shown that these markings are simply due to the ribs of the medullary cast, which have become impressed on the thin carbonaceous layer to which the external tissues are reduced (see WILLIAMSON, "Organization," Part I., 'Phil. Trans.,' 1871, p. 495).

Now as regards the general morphology, the simple leaves, arranged in whorls of many members, form an obvious point of resemblance to *Equisetum*. In the specimens of *Calamites* showing structure, we can, indeed, only infer the position of the leaves from that of the outgoing vascular bundles; the macroscopic specimens however, leave no doubt as to the facts.*

On the other hand, it is quite certain that the leaves were separate, not cohering to form a sheath, as in *Equisetum*. Further, the alternation of the leaves of successive whorls was less constant in *Calamites* than in the recent genus.

The *branches* of the stem in *Equisetum* are alternate with the leaves of the whorl, in the axil of which they arise. This agrees substantially with the position of the branches in *Calamites* (see Plate 72, photographs 5 and 6, Plate 80, fig. 21). The relation of the vascular bundles to those of the main stem seems also to agree in the two genera, but this will be considered below. The insertion of the branches *below* the node in *Equisetum* is, of course, only apparent. The branches arise in the axil of the whorl, and therefore above it. Subsequently they become overgrown by the leaf-sheath, and ultimately break through it at its base. If the leaves of *Equisetum* were distinct like those of *Calamites*, the insertion of the branches above the node would be equally evident in both genera.†

As regards the insertion of the adventitious *roots*, we know that in *Equisetum* they arise from the base of the lateral branches, one to six on each branch. From the specimens of *Calamites* showing structure, we have at present no evidence as to the insertion of the roots. There is, however, no doubt, from the evidence of impressions and casts, that the roots arose at the node or immediately above it, from the base of the internode. Sometimes they were placed in a regular circle, sometimes they are grouped in tufts, and these tufts may arise at the base of a branch.‡ It does not seem probable, however, that they had any constant relation to the branches, such as we find in *Equisetum*.

So far as our knowledge of the external morphology of the vegetative organs of *Calamites* extends, we thus find a general agreement with *Equisetum*, sufficient to be quite consistent with a relationship between the genera, but not by itself conclusive.

(1.) It has already been mentioned that in the course of the vascular bundles the resemblance to *Equisetum*, though evident, is incomplete; the differences consist in the facts that a bundle may traverse more than one internode, and that the bundles of successive internodes do not constantly alternate with one another (see Plate 72, photograph 5, and Plate 78, fig. 11).

* See especially WEISS, "Steinkohlen-Calamarien," II., 1884, cap. 3, "Beblätterung der Calamarien."

† *Cf.* JANCZEWSKI, "Recherches sur le Développement des Bourgeons dans les Prêles." 'Mém. de la Soc. des Sci. Nat. de Cherbourg.' XX., 1876. His principal figures are reproduced in the modern textbooks, such as those of GÖBEL or VAN TIEGHEM.

‡ WEISS, "Steinkohlen-Calamarien," II., 1884, cap. 4, "Wurzeln der Calamiten"; LINDLEY and HUTTON, 'Fossil Flora of Great Britain,' vol. 1, plates 78 and 79.

(2.) The arrangement of the vascular bundles in a single regular ring, enclosing a large pith-area, agrees well with *Equisetum*, but equally well with any normal Gymnosperm in Dicotyledon. We shall show in detail below that the canal at the inner edge of each bundle represents the disorganized protoxylem, so that in this respect the agreement with *Equisetum* is exact. We shall further show that in favourable cases there are distinct remains of the phloëm to the outside of the wood, so that there is no doubt as to the bundles being normally collateral, with centrifugal xylem, just as in the recent genus.

(3.) For the comparison of the minute histological structure, we are practically limited to the wood, and as only the primary region can be compared, the material is somewhat meagre. The primary xylem-elements of *Calamites*, the spiral, reticulated and scalariform tracheæ, are on the whole such as we find in *Equisetum*, and certainly agree less closely with those which we find in the corresponding position in other groups of vascular plants. The distinctive structure of the nodal, as compared with the internodal xylem, also shows a close agreement in the two genera.

In a few cases the structure of the cortex shows the distinct peripheral strands of sclerenchyma, which are frequent in the sub-aërial stems of *Equiseta*.*

To sum up our preliminary anatomical comparison. Although there is no secondary thickening, so far as we know, in any recent *Equisetum* (if we except the slight indications investigated by Mr. CORMACK)†, yet the primary structure, on which in the *Calamites* the secondary zone is superposed, is almost identical in the two genera.

PRIMARY STRUCTURE OF THE STEM.

a. *The Internodes.*

The first subject to be considered in detail is the primary structure of the stem. It is comparatively rare to find specimens in which this primary structure is unaltered. Where this is the case the specimens in question are usually, though not always, small twigs, with few vascular bundles. It must not be supposed that these twigs represent the earliest stages of the principal branches. They are probably ramuli of a high order, which in many cases seem never to have undergone any great degree of secondary thickening. In such small branches the pith is often solid,‡ just as is the case in the ultimate ramuli of some *Equiseta*, as, for example, *E. pratense*. In other

* See WILLIAMSON, "Organization," Part XII., 'Phil. Trans.,' 1883, II., Plate 33, fig. 19 (C.N. 62). NOTE.—Reference numbers preceded by the letters C.N. (= *Cabinet Number*) always indicate the number of the slide or specimen in the WILLIAMSON collection.

† "On a Cambial Development in *Equisetum*," 'Annals of Botany,' vol. 7, 1893.

‡ See WILLIAMSON, "Organization," Part IX., Plate 19, figs. 8 and 9 (C.N. 1 and 2). See also our own fig. 1, in Plate 77, though here the pith is not quite complete.

cases, however, the pith of these minute twigs is hollow.* It is impossible to doubt that in most cases, and apparently in all the larger branches, it soon became fistular in the living plant. This is shown both by the frequency and regularity of the casts of the medullary cavity, and by the very sharp limit of the outer persistent zone of the pith (see Plate 72, photographs 2 and 3, and Plate 77, fig. 3).

In a few cases specimens are preserved which evidently represent the young condition of branches of considerable size. The most striking of these is the *Calamopitus* described and figured in 1871.† Here there were about eighty vascular bundles, and though there had been some secondary formation of wood, its amount—about a dozen layers—is little in comparison with the dimensions of the stem. Other sections show from fifteen to twenty-one vascular bundles, with little or no secondary tissue. Early stages of development of the more considerable branches, are, however, much rarer than mere twigs, as we should expect.

In the arrangement of the vascular bundles, as seen in transverse section, we find the same variations as among species of *Equisetum* at the present day. While the most common type is one with the bundles rather near together, the primary medullary ray having a width scarcely greater than that of the bundle itself, we sometimes find the bundles much more scattered, and separated from one another by rays more than twice their own width.‡

Similar differences are found, if, for example, we compare *Equisetum pratense* with *E. limosum.*

In the earliest stages observed, the vascular bundles, so far as their primary structure is concerned, appear to be already fully formed. In all cases the fascicular canal is open and well defined,§ and in all cases, too, there is a strand of thick-walled elements bordering on the outer side of the canal (see Plate 72, photograph 1, Plate 77, figs. 1 and 2). It is not always easy, in a strictly transverse section of a very young stem, to see which elements represent the xylem. When, however, the section is rather oblique, so that the markings on the lateral walls of the elements can be distinguished, it becomes evident that the thick-walled cells on the outer side of each canal are tracheæ, and constitute the xylem-groups (see Plate 77, fig. 4).

The most important question relating to the vascular bundle in its primary condition concerns the nature of the canal which is always present on its inner margin. The presence of these canals, the *internodal* canals of previous memoirs, gives to the transverse sections an extraordinary resemblance in habit to corresponding sections of an

* Plate 72, photograph 1, and Plate 77, fig. 2; also WILLIAMSON, *loc cit.*, fig. 10.

† WILLIAMSON, "Organization," Part I., p. 488, Plate 25, figs. 19, 20, &c.

‡ See WILLIAMSON, "Organization," Part I., figs. 9, 14, 15, 20, 26. Our own figures are all of the former type.

§ We leave out of consideration some exceptional cases in which the canal is filled with a parenchymatous tissue. These will be discussed subsequently; here it need only be said that in such instances the filling of the canal seems to have taken place long after its formation.

Equisetum. Is this resemblance accidental, or are the two structures really homologous ? If the latter alternative be true, then the canal, in *Calamites* as in *Equisetum*, must represent a disorganized strand of protoxylem—the first-formed part of the wood of the collateral bundle. It is impossible to follow the development in the fossil; as already stated, the youngest stages preserved have their canals fully developed. All that we can expect is to find recognizable remains of the elements which originally filled the cavity; if these elements have the character of primitive tracheæ, then the homology with the carinal canals of *Equisetum* may be taken as established.

Happily, there is a long series of sections in the Williamson collection which serve to set this question completely at rest.

In every well-preserved transverse section it is common, or in fact the rule, to find isolated rings of about the diameter of a small trachea, within the canal. The resemblance of these annular fragments to the remains of tracheæ always seen in the carinal canals of *Equisetum* has long attracted our attention. The same point has been observed and figured by Mr. CORMACK,* who, we believe, was the first to publish the true interpretation. Occasionally, where the canal is small, these rings may collectively occupy the greater part of its area.† In some cases, also, we can trace a transition from the isolated rings in the canal itself, to the loosely arranged and partly disorganized tracheæ which abut on its outer margin.‡ Even in transverse sections the elements in the canal sometimes lie obliquely; in these cases we can see that the rings are placed one above another, as in an annular trachea, while sometimes we find portions of a spiral or a reticulated cell-wall. That we have really to do with the remains of tracheæ is evident. The tracheal remnants are most frequent towards the outer edge, or at the sides of the canal. For reasons which will appear immediately, they are less commonly met with at its *inner* edge. Transverse sections, however, can rarely afford by themselves conclusive evidence as to the nature of the elements contained in the canal. It is only when we examine a decidedly oblique section of a well-preserved specimen that all doubt is removed. Such a preparation is represented in Plate 77, fig. 4. The specimen is a corticated one, but the cortex has not been shown in the figure. Here the section is sufficiently transverse to show clearly the position of the canals, and at the same time sufficiently oblique to leave no doubt as to the character of the elements within them. Annular, spiral, or laxly reticulated tracheæ are evident in every canal, and sometimes extend to its inner margin. The gradual transition from these primitive tracheæ to the more scalariform elements towards the exterior can be clearly traced. Such a section is convincing by itself, but

* 'Annals of Botany,' vol. 7, *loc. cit.*, 1893.

† As in C.N. 19. We have thought it convenient, for the benefit of future investigators, occasionally to refer to the cabinet number of specimens in the Williamson collection other than those figured.

‡ As in C.N. 10, 1007, &c.

the study of accurately longitudinal sections is necessary in order to complete the argument.

Tangential sections passing through the primary wood of the bundles are of special value, as in them the position of the canals is clearly shown, and there can be no doubt that we are really examining the fascicular passages, and not any chance lacunæ. Such a section is represented in Plate 80, fig. 21. The part figured touches on two canals, and shows the partly disorganized protoxylem and primary xylem of two bundles.* In all such preparations, when sufficiently well preserved, remains of the primitive tracheæ are found in the canals and can be recognized at once, though more or less broken up, by their annular, spiral, or reticulated thickenings. By careful comparison of sections in somewhat different planes it is easy to prove that the innermost tracheæ of the solid xylem-strand are themselves somewhat disorganized, the disruption becoming much greater towards the interior, where the canal itself is reached.

Having become familiar with the appearances presented in oblique and tangential sections, the canals can easily be recognized with certainty in radial view.† (See Plate 77, fig. 5; Plate 78, fig. 10.) Where remains of tracheæ are found quite at the inner margin of the canal, they are usually of the annular type, with remote rings. Many of the elements are broken up in such a way that a series of several consecutive rings is left in position; then there is a gap, then another short series of rings, and so on. The nearer the tracheæ are to the inner side of the canal, the longer are the gaps, and the shorter the series of persistent rings. (See Plate 77, fig. 5.) Evidently here, as in *Equisetum*, the development of the primary xylem is centrifugal; the innermost elements have been differentiated earliest, and have consequently undergone the greatest amount of disruption during the extension of the internode. In many of the tracheæ the rings are connected here and there to form short spirals or reticulations.

In some cases, a radial section passes through a canal so as to show its termination at a node. Here it is clear that the protoxylem in the internodal canal is continuous with the *innermost* elements of the nodal xylem. This point is illustrated in Plate 78, fig. 10.

In no case, except where the preservation is bad, has a canal been examined in longitudinal section, without traces, at least, of the protoxylem being discovered.

From these observations we conclude: that the internodal canals of *Calamites* represent the earliest-formed xylem of the primary vascular bundles; that this primitive wood became disorganized and ruptured, owing to the longitudinal and transverse extension of the growing internode; and that the formation of the canal was due to a tearing of the tissue caused by the presence of a strand of inextensible lignified elements among the actively-growing parenchymatous cells.

* Other tangential sections showing the same facts are C.N. 24, 37, 38, 49, 91, 130*, and 1937.

† Especially good radial sections for this purpose will be found in C.N. 20, 20A, 21, 22, 48, and 1937.

In fact, all the evidence goes to show that the internodal canals of *Calamites* are identical in nature and origin, as well as in position, with the carinal passages of *Equisetum*. The demonstration of this homology is a considerable step towards establishing the essential agreement between the stem of a Calamite and that of an *Equisetum*.*

We will now go on to consider the structure of the remainder of the primary wood, *i.e.*, of those xylem-elements which lie on the outer side of the canal. Here we often find a difficulty in distinguishing between primary and secondary xylem. In transverse sections the regular radial series can often be traced inwards, as far as the canal, while, in other cases, the elements nearest to the latter are irregularly placed. Where all the tissue in question is radially arranged, such sections do not enable us to draw the line between primary and secondary wood. The same difficulty exists in many recent plants with an early development of secondary tissue.

Longitudinal sections, however, especially those in the radial plane, show us the elements which are characteristic of the primary xylem. The tracheæ just outside the canal are either densely spiral, or reticulated. Spirals capable of unrolling seem only to occur in the protoxylem of the canal itself. Scalariform tracheæ come next, or may themselves adjoin the canal. (See Plate 77, fig. 5; Plate 78, figs. 7 and 10.) Their pits are bordered, as in similar elements of recent plants. This is shown in fig. 9A, on Plate 78, which is taken from a tangential section passing so near the pith that we regard it as showing the structure of the primary wood. Where one of the tracheæ is in contact with a parenchymatous cell, the pits are only bordered towards the tracheæ, just as in so many recent plants. Short parenchymatous cells are embedded here and there among the tracheæ. The latter seem to be tracheides, but further histological details will be more conveniently considered when we come to the secondary wood.

The sections of the very young stems afford little information as to the phloëm, which is in no case preserved in such specimens. There is, however, no doubt that the bundles were collateral. In all the corticated specimens there is a gap between xylem and cortex, which is only obliterated where the latter has evidently been crushed in upon the former. (See the various transverse sections shown on Plates 72, 77, and 78.) In this gap, disorganized carbonaceous matter, sometimes showing signs of cellular structure, is present. In very early stages (see Plate 77, fig. 2) the interfascicular tissue is sometimes continuous from pith to cortex, but more usually it is interrupted by a disorganized layer, which presumably represents the delicate pericyclic tissue from which the interfascicular cambium would have arisen.

The preparation which shows the most satisfactory remains of the phloëm, is one from which photograph 3, on Plate 72, and figs. 12, 13, and 14, on Plate 78 are taken. In the group shown in fig. 13 the whole tissue, though much crushed, is preserved

* After the above was written, Count SOLMS-LAUBACH very kindly lent us some beautiful sections of a Calamite from Halifax, which afforded additional evidence of the facts just stated.

from cambium to cortex. Similar groups can be seen at several points of the section, and the preservation is sufficiently good to show that the phloëm was formed in greater abundance opposite the primary bundles than in the interfascicular regions. The regular brick-shaped cells seen in fig. 14, are either cambium, or at least derivatives of the cambium, which have retained their original form. This specimen is one which already has a broad zone of secondary wood, about twenty-five cells in radial thickness.

The external limit of the vascular cylinder is always quite sharp. This is due, however, to the almost constant presence of disorganized tissue on the boundary-line, not to the differentiation of any evident limiting pericycle. As to the presence of such a layer we have very little direct evidence. In the rare cases where the phloëm is preserved, we sometimes find one or more layers of larger, thin-walled cells at its periphery (see fig. 13); these may have belonged to the pericycle.

As regards the structure of the primary *cortex*, we find considerable variations among the comparatively few corticated specimens which are preserved. In the smaller twigs there is but little differentiation. The whole thickness of the cortex is made up of parenchyma, in which a few elements with thicker walls are scattered. (See Plate 72, photograph 1; Plate 77, figs. 1 and 2). Some of the cells have especially abundant carbonaceous contents, and may possibly represent secretory sacs.

In other branches, of somewhat greater diameter, a more differentiated cortex is present, consisting of an inner and an outer zone, of distinct structure. (See Plate 72, photographs 2 and 3; Plate 77, fig. 3; Plate 78, fig. 12.) In all these cases the inner zone is characterized by larger cells, with thinner walls, than those of the outer region. In the specimen illustrated in photograph 3, and fig. 12, in which the cortex is remarkably well preserved, the outer zone is itself differentiated, its cells becoming smaller and more sclerotic towards the periphery. The supposed secretory sacs may occur in any parenchymatous part of the cortex. We find, however, no indication of intercellular secretory *canals*.

In a third type, already referred to, the outer cortex has sharply defined, wedge-shaped bands of sclerenchyma, alternating with thin-walled tissue. (See WILLIAMSON, "Organization," Part XII., Plate 33, fig. 19, from C.N. 62.)

The more complex cortex seems to be characteristic of the somewhat larger branches; the number of corticated specimens is, however, too small to admit of any safe generalization.

A definite endodermis at the inner margin of the cortex has not been detected with certainty. In several preparations however, the innermost cortical layer, where preserved, consists of regular, thin-walled cells, fairly distinct from the rest of the tissue.

The above description sums up what we know of the primary structure of the internode. We have next to consider the modifications of structure presented by the

nodes, and in connection with this subject to examine, more fully than we have yet done, the longitudinal course of the vascular bundles.

b. *The Course of the Vascular Bundles and the Structure of the Nodes.*

In considering the question of the longitudinal course of the vascular bundles, it is obviously necessary to start from specimens in which we know for certain which is the upper and which the lower end. A specimen for which the cabinet is indebted to Mr. WILD affords this evidence in a very convincing manner. The branch in question has a pith which tapers rapdily at one end; a series of eight transverse sections were cut from this part, three of which are shown in the photographs 7, 8, and 9, on Plate 73. We shall return to these sections later; here we need only point out that the *base* of the branch is the end at which the pith has its *minimum* diameter. That this is so has long been proved: it is sufficient to refer to our figures, Plate 79, fig. 20, and Plate 80, fig. 22; to the figures 27 and 30 in Part IX. of WILLIAMSON'S series of Memoirs in the 'Philosophical Transactions,' 1878, Part II.; and to Plates 2, 3, 4, &c., in WEISS'S 'Steinkohlen-Calamarien,' Part II. From the upper part of Mr. WILD'S specimen a longitudinal section has been cut (C.N. 1937), on which the upper and lower ends are marked. A part of the section is approximately tangential, and shows the course of the bundles with perfect clearness, so that here we have the desired evidence in an unmistakeable form. The same section shows further that the lateral branches were inserted immediately *above* the node. We can, therefore, use this fact as a means of orientation in other cases; in all sections which show branches we know that the adjoining node is *below* the branch, and thus the top and bottom of the specimen are determined. Another useful clue is afforded by the fact that the outgoing foliar bundle is generally situated in the median line of the bundle running up to it from *below*, while this is seldom the case with the bundles above the node.* Another indication which can sometimes be made use of is the fact that the xylem of the stem-bundles is directly continuous with that of the outgoing leaf-trace, from *below* only. On the upper side the tracheæ overarch the leaf-trace bundle, but are generally separated from its xylem-elements by some parenchymatous tissue. (See Plate 78, fig. 8.) These latter indications (to which others might be added) are of service where there are no branches to afford a more certain guide. When we have once become familiar with the structure of specimens in which the direction is known, there is seldom any difficulty in determining the position of apex and base in any case where we have a tangential section through the wood.

In Mr. WILD'S specimen, and in some others, the course of the bundles is essentially that of *Equisetum*. If we trace any bundle from below upwards, we find that at the

* This indication, however, can only be trusted where the tangential section passes very near to the pith. The width of each woody wedge increases towards the exterior, and this increase is not always symmetrical with reference to the leaf-trace bundles.

node it bends out in a horizontal direction, forming the foliar bundle, which is therefore cut transversely in a tangential section. At this point branch-bundles are given off to the right and left, which unite with the corresponding branches of the neighbouring strands, and thus constitute the bundles of the next internode above. Here, therefore, we have a regular alternation in successive internodes, and each leaf-trace extends through one internode only. This simple arrangement is, however, by no means constant. Thus, we often find the bundles of adjacent internodes lying nearly in the same straight line; the forks of a bundle at the node curve round the outgoing leaf-trace, and unite on its opposite side (see one of the bundles in photograph 5, on Plate 72). This may occur in the same specimen which in other parts shows regular alternation.*

In other cases, the bundles at the node are about twice as numerous as the outgoing foliar bundles—or, in other words, only about every alternate bundle passes out at a given node. (See Plate 78, fig. 11.) Here each bundle must pass through two internodes, instead of one, before joining on to the trace of another leaf. In all the tangential sections, including those of *Calamopitus,* similar variations occur.†

We may sum up the facts considered as follows:—The bundle-system of *Calamites* bears a general resemblance to that of *Equisetum.* A single leaf-trace enters the stem from each leaf, and passes vertically downwards to the next node. In the simplest cases the bundle here forks, its two branches attaching themselves to the alternating bundles which enter the stem at this node. In other cases both the forks attach themselves to the same bundle, so that, in this case, there is no regular alternation. In other cases, again, the bundle runs past one node without forking, and ultimately forms a junction with the traces of the *second* node below its starting-point. These variations may all occur in the same specimen. The xylem at the node usually forms a continuous ring, for, where the regular dichotomous forks of the bundles are absent, their place is usually taken by anastomoses. Occasionally, however, the ring is interrupted. (See photograph 5, on Plate 72.)

The nodal xylem, *i.e.*, the commissural ring of primary wood, composed of the forks and amastomosing branches of the bundles, differs considerably from the primary xylem of the internode. In the first place, the former is much greater in amount than the latter. The nodal wood projects conspicuously into the pith, forming the well-known constriction, so familiar in the medullary casts. It is also somewhat prominent on the outer side, so that the secondary tracheæ deposited upon it are arched outward at the node, as has often been described in former memoirs.‡ (See Plate 72, photograph 4; Plate 78, figs. 7 and 10.) It may, indeed, be questioned whether this mass of wood at the node is properly to be regarded as altogether

* As in C.N. 20, A and B, 24, &c.

† See WILLIAMSON, "Organization," Part I., Plate 26, fig. 25, &c. In these figures *m* indicates the foliar bundle.

‡ See WILLIAMSON, "Organization," Part I., p. 483.

primary or as mainly secondary. No sharp line can be drawn between the short and somewhat irregularly arranged tracheæ of the nodal wood, and the longer elements with definite radial seriation, which the cambium has added on their outer side. We prefer, however, to regard the short-celled wood of the node as primary, and that for two reasons: (1) in very favourable preparations (see, for example, Plate 78, fig. 10) we see that the nodal wood is continuous with the primary wood of the adjoining internode; (2) in recent *Equiseta* an exactly similar mass of wood is developed at the nodes, as we have seen especially well in preparations of *E. pratense.** Additional evidence in favour of the primary nature of the nodal xylem is afforded by the anatomy of the axis of the strobilus in the Calamitean fructification described in the previous memoir.† Here the tissue in question is fully formed in an organ which is without secondary thickening. At the node the tracheæ are relatively short, and have a more or less oblique position with reference to both the radial and tangential planes. They may even be nearly horizontal, especially in the neighbourhood of the outgoing foliar bundle.

The cell-walls of the nodal tracheæ are often reticulated or pitted, while those of the adjacent elongated tracheæ of the internode are scalariform. Sometimes this difference is very conspicuous. Some of the pith-cells bordering on the wood of the node are also conspicuously pitted.

As regards the mode of exit of the foliar bundles we already know that they bend out almost at a right angle with the axis (see Plate 72, photographs 5 and 6; Plate 77, fig. 6; Plate 78, figs. 7 and 8). Our knowledge of their structure is limited to their xylem, for we have no specimens to show the leaf-trace bundles passing through the cortex, where alone their phloëm could be shown. Their tracheæ often have a typical spiral thickening; sometimes their walls are reticulated or scalariform (figs. 6 and 7). They are accompanied on their outward course by some parenchymatous elements. As already mentioned, the xylem of the foliar-bundle is continuous with the protoxylem of the stem-bundle which forms its downward prolongation.

It is evident that during the formation of secondary wood the elements of the foliar-bundle must have been subject to tension and consequent rupture. In spite of this they can be traced for a long distance through the wood of old stems, especially in tangential sections, though they become very hard to find in the outer layers. It is possible that elements may have been added to them for some time, by the cambium.‡

Apart from the irregularities of distribution already sufficiently dwelt upon, we may say that the structure and arrangement of the primary vascular bundles in *Calamites* present an agreement with those of *Equisetum*, which could scarcely be closer than it is.

We have for the present left the lateral branches out of account, although they

* Mr. CORMACK regards the nodal wood of *Equisetum* as being itself partly secondary. See his paper above cited. We do not think this view will hold good for the whole genus.

† WILLIAMSON, "Organization," Part XIV., 'Phil. Trans.,' vol. 179, B., 1888, Plate 10, fig. 5.

‡ *Cf.* STRASBURGER, 'Histologische Beiträge,' vol. 3, p. 121.

obviously formed part of the primary structure. All the preparations which we have, showing the insertion of branches, are sections of comparatively advanced stems, in which the secondary growth in thickness has already made considerable progress. Hence the structure of the branch-bases is much complicated, owing to changes connected with the formation of secondary wood, and until the latter has been studied in detail, the phenomena presented by the branches cannot be understood.

The Secondary Tissues.

So far as the first origin of the secondary tissues is concerned, the type of development in *Calamites* always corresponds to the simplest of the various modifications with which we are acquainted in recent Dicotyledons and Gymnosperms.* We have only to distinguish between *fascicular* and *interfascicular* tissue, the former including all the tissue developed within the limits of each primary bundle, while the latter arises by the division of cells belonging to the primary medullary rays. In no case is there any preliminary formation of intermediate cauline strands, as so frequently happens among Dicotyledons. The secondary thickening of *Calamites*, in fact, so far as concerns its earlier stages, is of diagrammatic simplicity (see Plate 72, photographs 1, 2, and 3; Plate 77, figs. 1, 2, and 3).

As soon, however, as the zone of secondary tissue begins to attain any considerable thickness, variations make their appearance, depending chiefly on the degree in which the fascicular and interfascicular strands remain distinct in the secondary region, or in other words, on the part played by the principal medullary rays† during secondary growth.

Among the specimens examined by us we find four distinct types as regards this point. These distinctions are, of course, purely anatomical, and may have little or no systematic value. We may group the various forms as follows :—

A. Principal rays remain parenchymatous throughout the whole thickness of the secondary wood.

As sub-divisions of this type we have :

A 1. The ray maintains about the same thickness throughout.

A 2. It becomes narrowed towards the exterior by the greater tangential growth of the fascicular wood.

B. The principal rays disappear, as such, towards the exterior, owing to the formation of interfascicular wood.

* See De Bary, 'Comparative Anatomy of Phanerogams and Ferns,' English Translation, p. 455, &c.

† We propose to limit the term *primary* ray to the truly primary interfascicular tissue. When this is prolonged into the secondary tissues by the cambium, we speak of it as a *principal* ray; the term *secondary* ray is applied, as usual, to those intermediate rays, which are entirely of cambial origin.

As sub-types we have :

B 1. The change takes place suddenly, the interfascicular wood at once extending across the whole width of the ray.

B 2. It takes place gradually, the ray becoming narrowed and subdivided by the formation of new strands of tracheæ, both at the sides, and in the middle of the ray.

The sub-type A 1 is exceptional among our specimens. We have examined stems* with wood about eighteen elements in radial section, in which the rays are certainly parenchymatous throughout and do not diminish in thickness. Tangential sections of this type of stem† leave no doubt of the purely parenchymatous structure of the principal rays. In no case, however, is the stem of any considerable age, so we cannot be certain that the condition is anything more than a transitory one, and it is quite possible that at a later stage interfascicular wood might have been formed.

The peculiar form described in former memoirs under the name of *Calamopitus*,‡ may either come under this head or under B 1. Here the interfascicular tissue does not appear to contain true tracheides, but the elements are very prosenchymatous, so that the character of the tissue is totally different from that of ordinary parenchymatous rays. The prosenchymatous ray-cells of *Calamopitus* have no visible pits on their walls, and cannot well be classed as tracheides ; they differ from the tracheides in the wood of the same plant in shape and size, for the ray-cells are somewhat shorter and decidedly broader. In tangential sections, small parenchymatous secondary rays, sometimes only two cells in height, are seen between the prosenchymatous elements of the interfascicular tissue, like those between the tracheides of the fascicular wood.§ The whole structure shows a decided approach to that of *Calamodendron* BRONGR., of which we have examined some beautiful sections cut from a specimen found in the Permian of Chemnitz, and kindly presented to the collection by Count SOLMS-LAUBACH. *Calamodendron,* however, is not known to occur in the English coal-measures, and we have not included it in the present paper.

We think the genus *Calamopitus* should be retained. Besides the peculiar structure of its principal medullary rays it is characterized by the predominance of reticulated elements in its wood, by the characteristic arch-like form of the commissural bundles at the node (as seen in tangential section), and by the very large and definite "infranodal canals." Further information from additional specimens is however much needed.

The sub-type A 2 is a very unimportant one, and has only been observed in two very small Calamitean stems, with wood not exceeding seventeen elements in radial

* *E.g.*, C.N. 13 and C.N. 18.

† *E.g.*, C.N. 33.

‡ WILLIAMSON, 'Mem Lit.' and 'Phil. Soc.,' Manchester, ser. 3, vol. 4, 1869. "Organization," Part I., 1871.

§ As in C.N. 54.

thickness.* Here the principal rays narrow out rapidly towards the exterior, the marginal series of the ray dying out altogether, while the more median rows become attenuated. These changes appear to be due to the vigorous tangential growth of the elements of secondary fascicular xylem; there is no formation of interfascicular tracheides, the ray being wholly parenchymatous throughout.

The great majority of the specimens investigated belong to the type B, with interfascicular wood. In some cases (sub-type B 1) the principal rays come almost at once to a sudden end; little or no secondary interfascicular parenchyma is formed, and the interfascicular wood immediately assumes, so far as the transverse section shows, the same structure as the fascicular wood, appearing to consist of radial strands of tracheides, with narrow secondary rays, usually only one cell in breadth, between them.†

This case, however, though frequent, is exceptional. In the great majority of our English specimens the principal rays narrow gradually towards the exterior, the interpolation of interfascicular series of tracheides taking place step by step. This, the prevalent case (sub-type B 2, in the arrangement adopted), is the one which we have been able to study most in detail. It will therefore be best to base our description on stems of this variety (see Plate 72, photographs 2 and 3, Plate 77, fig. 3‡).

With the exception of *Calamopitus*, all our English specimens would probably fall under GÖPPERT's genus *Arthropitys*, which is simply a synonym of *Calamites*, as we propose to limit that genus. The forms which we are about to consider may be taken as the type of *Calamites* in the above sense. Count SOLMS-LAUBACH has pointed out the urgent need for further investigation of the structure of the wood in Calamarieæ.§ So far as the typically Calamitean structure is concerned we are now in a position to supply fairly complete information, the preservation of many of the specimens from the English coal-fields being so perfect that the structure can be studied nearly as well as in a recent wood.

The earliest stages of secondary growth scarcely need any further description. In fig. 1, on Plate 77, we have a transverse section of a stem, in which the very first tangential divisions have taken place in the interfascicular tissue, while the very definite radial seriation of the xylem of the bundles indicates that here also cambial activity has begun. This is in a twig about ·7 millim. in diameter—the smallest yet observed. Another specimen, two sections of which are shown in photograph 1, on Plate 72, and in fig. 2, on Plate 77, though of larger size, shows scarcely a trace of any addition to the primary structure. In the bundles themselves there was pro-

* Shown in some new sections not yet incorporated in the collection.

† See WILLIAMSON, "Organization," Part I., Plate 24, fig. 15. WEISS, 'Steinkohlen-Calamarien,' Part II., p. 10, fig. 3. Shown in C.N. 15, 16, 17, one section in 118*, &c. Good longitudinal sections of this form are still required.

‡ See also WILLIAMSON, "Organization," Part I., figs. 9, 14, 16, 17, 26.

§ 'Fossil Botany,' English translation, p. 298.

bably no definite interval between the primary and secondary tissue-formation, hence it is convenient to take the interfascicular divisions as marking the commencement of secondary growth. In fig. 2 then, we have a stage immediately before, and in fig. 1, a stage immediately after the beginning of cambial increase. We can scarcely expect to fix the starting-point more exactly than this.

In describing the secondary tissues we will begin with the fascicular wood. The elements are arranged with remarkable regularity in radial series. Passing from within outwards, the number of the series gradually increases, by the occasional duplication of a row, but the regularity of the tissue is always maintained.

In good transverse sections we can easily see that the wood consists of two kinds of elements; the majority of the radial series are composed of relatively large elements, with rather thick walls, while other rows, between the former, consist of narrower cells, with thinner walls (see Plate 72, photograph 3; Plate 77, fig. 3; Plate 78, fig. 12, &c.). The comparison of tangential and radial sections show that the former elements are tracheæ, the latter constitute small secondary medullary rays (see Plate 72, photograph 6, also WILLIAMSON, "Organization," Part I., Plate 23, fig. 5; Part IX., Plate 20, fig. 16). As we advance from within, outwards, we find that the number of these secondary rays increases, new ones making their appearance successively, just as happens in the secondary wood of a Gymnosperm or a Dicotyledon. Most often the secondary rays are one cell only in breadth, frequently they are two cells broad, sometimes more. The radial diameter of their cells is equal to, or somewhat greater than that of the tracheæ; their tangential diameter is much less. The height of the ray-cells is generally their greatest dimension, so that they belong to the "upright" type of DE BARY.* In other cases, however, the ray-cells are approximately square, as seen in radial section, and the two kinds of elements may occur in the same ray. Uniseriate rays (only one cell in height) are very common; their form, as appearing in a tangential section, is lenticular.

The proportion of tracheæ to secondary rays varies in different specimens; the tracheal series, however, are always the more numerous.

As regards the nature of the tracheæ, the most important question which we have to decide, is whether they are true vessels or tracheides. These elements are of very considerable length, and have very oblique terminal walls, inclined to the radial plane at an acute angle (see figs. 16 and 17, on Plate 79). It is not an easy matter to measure their length, as the whole trachea is not often included in the plane of section, and it is only in the best-preserved specimens that it is even possible to determine whether this is the case or not. We have, however, succeeded in making some measurements. In a tangential preparation (C.N. 20 B, from part of which fig. 8 on Plate 78 was drawn), five tracheæ were measured; their length varied from 1·7 to 2·4 millims., the average being about 2 millims. This, however, is much exceeded in other cases. In another tangential section, perhaps the most perfect in the collection

* *Loc. cit.*, p. 486.

(C.N. 1554, from which photograph 6, on Plate 72 was taken), we measured two tracheæ, the lengths of which were almost the same, namely 4·1 and 4·2 millims. This is just equal to the maximum length of the tracheides in *Pinus*.* In the fascicular wood the tracheæ run approximately vertically, with only trifling curvatures.

We have found it a very general rule that the pits in the secondary tracheæ are limited to their radial walls. This statement is based on the evidence of all the tangential sections which are sufficiently well-preserved to show the structure in detail. The absence of pits on the tangential walls cannot be merely apparent, or due to imperfect preservation, for the same tangential sections, which show no pits in surface view, present quite obvious pits, seen in section, on the radial walls of the tracheæ (see Plate 78, figs. 8 and 9), while radial sections of the same specimens, show the pits in surface view with perfect clearness (see Plate 78, figs. 7 and 10).† We regard the establishment of this fact as of considerable interest, for it indicates that the mechanism for the passage of sap through the wood of *Calamites* was of the same kind as that existing in recent Coniferæ. Such a character is, of course, of no *systematic* value, as is shown by the well-known case of *Drimys* among the Dicotyledons.‡

It is only in the most internal part of the fascicular wood, immediately outside the canal, that we find tangential pits on the tracheæ. They were either limited to the primary xylem, or at most extended to a few of the first-formed secondary layers (see Plate 80, fig. 21). As already mentioned, the peculiar short-celled wood at the nodes has pits on all surfaces of its elements, but we have already given reasons for regarding this wood as primary.

The pits on the radial walls are sometimes of the scalariform type, that is, they are transversely elongated, so as to extend across the whole width of the wall; in other cases they are shorter, having an elliptical outline. More than one row of pits may be present on the same radial wall. In some radial sections it appears that the scalariform pitting is limited to the more internal tracheæ, sometimes even to those which may be regarded as primary, while all the pits seen on the more external tracheæ are of the shorter form. This, however, is not a constant rule. For example, in the largest specimen of which we have examined sections,§ the scalariform type of thickening prevails in all parts of the wood, which is 2 inches thick, though tracheæ with shorter pits are seen here and there. As the nature of the pitting may vary in different parts of the same trachea, we attach little importance to these differences. They probably depend in part on the relative positions of the tracheæ. Where the elements in two adjacent radial rows correspond, so as to be in contact with each other by their entire radial surfaces, we generally find scalariform pitting. Where, however, the elements

* See DE BARY, *loc. cit.*, p. 506.

† The preparations on which these statements are chiefly based are, C.N. 20, 20A and B, 21, 22, 65–68, 83-87, 88–91, 130* and 131*, and 137*, 138*, 1554, and 1937.

‡ See STRASBURGER, 'Histologische Beiträge,' vol. 3, p. 161.

§ The radial section is C.N. 80. See WILLIAMSON, "Organization," Part IX., Plate 20.

overlap, so that each trachea abuts on portions of two others in the next row, we find the shorter pits.

Where tangential pits are present, *i.e.*, on the walls of the more internal tracheæ, they are usually scalariform. Sometimes a few oval pits are seen on the tangential walls in the transitional region, before they disappear altogether.

The very oblique terminal walls of the tracheæ have similar pits to those of the radial walls, from which indeed they are in no way marked off.

In tangential sections we frequently find the pits well shown in sectional view.* In all cases they are evidently bordered, the thickened ridges distinctly over-arching the delicate closing membrane, which is, of course, only preserved in the most favourable cases. Between two tracheæ the pits are bordered on both sides; between a trachea and a cell belonging to a medullary ray, whether principal or secondary, we find one-sided bordered pits, the border being on the side towards the trachea. (See Plate 78, fig. 9, A and B.)

From the general form of the tracheal elements, and especially from their tapering ends, the impression is strongly conveyed that they are tracheides and not vessels. Their oblique terminal walls have the same pitted structure as the lateral walls, and there is no evidence that the pits were perforated in either case, though, of course, it is impossible to prove that this never happened. Direct evidence of the development cannot be expected from a fossil, but when we come to consider the interfascicular wood we shall find some facts which speak strongly for the origin of each trachea from a single cell. There is no reason to doubt that the same mode of origin held good for the fascicular tracheæ.

In exceptional cases, however, we have found occasional traces of transverse walls in the tracheæ. Though such traces are sometimes doubtful, they are not always so. In a very few instances† the transverse wall is unmistakeable, and indeed seems to have formed a permanent septum. It must be understood, however, that such indications of septa are extremely rare, only occurring in certain preparations, and in a few tracheæ in each case. In those tracheæ which show the transverse walls, their position is quite irregular. We by no means believe that this casual appearance of an occasional septum points to the origin of the tracheæ by cell-fusion. It is doubtful whether the septa, when present, were ever absorbed at all. Two explanations are possible; either the young tracheide, while still a living cell, occasionally underwent septation, as is sometimes the case with sclerenchymatous fibres,‡ or else these transverse walls are not normal, but mark the limit between the cells of a thylosis.

There is no evidence for the existence of any xylem-parenchyma, apart from the medullary rays, in the secondary wood. Radial sections are decisive on this point, for all the parenchymatous cells manifestly form part of radial plates of muriform

* They are shown in great perfection in C.N. 20A and B, 137* and 138*, 1554 and 1937.

† Such an instance occurs in C.N. 138*.

‡ See DE BARY, *loc. cit.*, p. 134.

tissue, or at least (*i.e.*, in the case of uniseriate rays) form continuous radial series. The fascicular wood consists of tracheæ and medullary rays only.

The great differences in shape between the cells of the medullary rays suggest the possibility of a physiological differentiation, such as has been found by STRASBURGER in certain Dicotyledons, in which the upright and horizontal elements of the rays differ considerably in structure, and presumably in function also.* But we have no evidence of this in the fossil. Neither have we any reason to suppose that tracheides were present in the secondary rays, as is the case in the Abietineæ, although the general absence of tangential pits in the secondary wood might have led us to expect such an arrangement.† Only the nature of the pitting can guide us in such a question, and the evidence available is not conclusive, for such details can only be adequately studied in the best preserved specimens.

Pits on the walls separating the cells of the medullary rays from one another are seldom shown at all clearly. These cells usually have rather thin walls, and such pits as they may have had could have been of no great depth.

It now remains for us to consider the structure of the principal medullary rays, and more especially to investigate the process by which, in most of our specimens, they become bridged over by interfascicular wood.

The principal rays in the type (B 2) which we are now considering are of maximum breadth next the pith, and taper off rapidly (as seen in transverse section) towards the exterior (see Plate 72, photographs 2 and 3; Plate 77, fig. 3). The width of the inner end of the principal ray is much increased, in the older specimens, by the tangential dilatation of the more internal cells of the ray.‡ We find this phenomenon in many of the older stems,§ but its occurrence is inconstant; the dilatation may take place in some rays and not in others, within the same transverse section. The tangential width of a dilated ray-cell may amount to ·25 millim. or more, which is from two to three times that of the neighbouring unaltered cells. It is the middle cells of the ray which become dilated; those adjoining the wood on either side remain unaffected. It is evident that so considerable an extension of the width of the medullary rays allowed of a perceptible enlargement of the pith-area during the earlier stages of secondary growth. It is probable that the circumference of the pith may have increased in this manner to $1\frac{1}{2}$ times its original extent, or even more.

It can be proved that the tangential extension of the inner ray-cells was an active process, and not simply due to the tensions set up by the growth of other tissues. This is shown by the fact that the dilatation of the rays sometimes led to the crushing of the wedges of fascicular wood between them, and thus to the obliteration of the

* STRASBURGER, 'Histologische Beiträge,' vol. 3, p. 209.

† See STRASBURGER, *loc. cit.*, p. 9.

‡ See the figure in WILLIAMSON, "Organization," Part I., Plate 27, fig. 26, which, however, only shows a small degree of dilatation compared with many larger stems.

§ As in C.N. 133,* &c.

protoxylem canals.* This is a familiar process in recent plants, where parenchymatous tissues show active dilatation; we may specially cite the case of the tuberous roots of *Thladiantha,* formerly described by one of us.†

The structure of a principal medullary ray, as seen in a tangential section cut near the pith, is fairly constant in the various specimens examined. The middle rows of cells of the ray, varying in number in different cases from 2 to 8 or more, are short, often isodiametric, and sometimes tangentially dilated. The cells at the margins of the ray, adjoining the fascicular wood, are much elongated, but generally have square ends, like the rest (see Plate 79, fig. 15). If another tangential section, a little further to the exterior, be examined, we find that the principal rays are narrower; the elongated marginal cells have pointed ends, or are replaced by tracheides. The middle short-celled part of the ray shows little change (see Plate 79, fig. 16). A third section, taken still further towards the outside of the wood, shows a more profound change of structure. The principal rays are here no longer continuous throughout the internode, but are partitioned up into a number of short, lenticular rays by tracheæ, or strands of tracheæ, which cut obliquely through the original ray (see Plate 79, fig. 17). The same process is carried still further as we advance yet more towards the exterior, until, in some cases, the principal rays can scarcely be recognized any more, but are completely broken up into short rays, one or two cells in thickness, which differ but little from the secondary rays of the fascicular wood.‡

The comparison of transverse sections confirms the above observations. Tracing the radial cell-series of the principal ray outwards, we find, not only that the marginal rows of parenchymatous elements are succeeded by rows of tracheæ, but also that new rows of tracheæ make their appearance at various places in the interior of the ray. The latter sometimes appear to form the direct outward continuation of parenchymatous series, while sometimes they are interpolated between them; in the second case some of the parenchymatous radial series die out altogether.§

Favourable radial sections, which exactly follow the course of a principal ray, may also show how the more elongated parenchymatous cells are succeeded, towards the exterior, by tracheæ.||

There are many variations in detail; sometimes, for example, all the cells of the ray become more elongated towards the exterior of the wood. A more important

* This is very conspicuous in C.N. 123*, where the inner part of each strand of wood is quite crushed. [This evidently took place during life, for the rest of the tissue, including the dilated ray-cells, is perfectly preserved.]

† SCOTT and BREBNER, "Internal Phloëm in Dicotyledons," 'Annals of Botany,' vol. 5, 1891.

‡ The above outline description is founded primarily on the series C.N. 65–68, from which the figures are taken, and has been confirmed by the study of several other series, as C.N. 20A and B, C.N. 83–87, C.N. 88–91, C.N. 130* and 131*, and C.N. 137* and 138*, as well as by that of single tangential sections, which are scarcely less instructive, when, as often happens, they are very slightly oblique, so as to pass gradually from an inner to a more external region of the wood, as in C.N. 1937, &c.

§ See especially WILLIAMSON, "Organization," Part I., Plate 25, figs. 17 and 18.

|| As in C.N. 132***.

fact is, that as we trace the ray outwards we often meet with elongated cells of prosenchymatous form, but apparently without pits (see fig. 16). Such cells are most often found at the margins of the ray, but also occur in its interior. We must regard these prosenchymatous elements as intermediate forms between ray-cells and tracheides.*

The study of transverse sections shows us that the intruding tracheides, whether appearing at the sides or in the middle of the ray, are not isolated, but form, almost from their first origin, continuous radial series.†

The question now arises how this interfascicular wood which we have described is developed. The principal medullary rays consist of relatively short cells, which, judging from the analogy of recent plants, must have arisen from cambial cells of like form. Now the difficulty is, that wherever interfascicular tracheæ appear, we find these short elements replaced by extremely long ones. A numerical estimate of this difference has little value, in view of the great variations in length of both ray-cells and tracheides, but in many cases we may safely assume that the interfascicular tracheides are twenty times as long as the parenchymatous cells of which they take the place. Yet the radial seriation of the elements is scarcely disturbed by this enormous change in their dimensions. "Sliding growth" to such an extent would inevitably bring with it a complete obliteration of the original radial arrangement of the secondary tissues.‡

The hypothesis that the interfascicular tracheæ arose by cell-fusion is at first tempting, but there is no sufficient evidence to support it. We have already discussed the rare cases in which there are traces of transverse walls; in the vast majority of tracheæ nothing of the kind is visible. There is no analogy among recent plants for the existence of xylem-vessels without any trace of the limits of the cells from which they are formed.§

The sculpturing of the cell-wall is so often perfectly preserved in the fossil *Calamites*, that remains of transverse walls can scarcely have escaped observation, considering how obvious they are wherever they exist in recent plants.

Besides this negative evidence, the existence of elements intermediate in form and length between the parenchymatous cells of the ray and the tracheæ is a strong argument for the origin of the latter by growth rather than by cell-fusion, especially as these transitional elements appear just where they are wanted, namely, where the interfascicular wood is beginning to form.

The solution which we suggest is that the interfascicular tracheæ arose by the

* They are well shown in C.N. 20B, 83, 90, and 130*.

† See WILLIAMSON's figure above cited, Part I., Plate 25, fig. 17.

‡ *Cf.* DE BARY, *loc. cit.*, p. 470; KRABBE, 'Das Gleitende Wachsthum,' 1886.

§ *Cf.* DE BARY, *loc. cit.*, p. 165. The case of *Dracæna* and its allies which might once have been supposed to afford such an analogy, is now known to be one of sliding growth (see SCOTT and BREBNER, "Secondary Tissues in Monocotyledons," 'Annals of Botany,' vol. 7, 1893).

elongation of single cells, but that this elongation took place in the cambium-cells before the tracheæ were cut off from them. We may suppose that an ordinary short cambial-cell, belonging to a principal ray, before beginning to produce tracheæ instead of ray-cells, itself became elongated by sliding growth. The existence of intermediate forms renders it probable that this elongation did not take place all at once. It is probable that a cambial-cell, after growing to some extent in length, divided, and cut off a short tracheide or transitional element; before the next division the cambial-cell may have grown to a greater length, and then have cut off a longer tracheide, and we may suppose this process continued until the interfascicular cambial-cells attained a nearly constant length, after which the development would go on uniformly, as in the fascicular wood.

This account of the process is, of course, only a hypothesis, for the direct observation of the successive stages of histological development is impossible, even in the best-preserved fossil. We think, however, that our hypothesis is one which explains the facts, and we do not see how the great elongation of the tracheides can be reconciled with the preservation of radial seriation in any other way.

A certain small additional amount of sliding growth may also have taken place in the young tracheides themselves, after their separation from the cambium, just as is known to happen in *Pinus.** The existence of occasional intruding ends of elements, presumably tracheides, seen in transverse section among the cells of the ray, renders this probable.

We have not had an opportunity of making a similar study of the type (our sub-type B1) in which the interfascicular wood at once bridges over the entire width of the principal rays. Probably a like explanation would apply here also ; we need only suppose that a larger proportion of the cambial cells forming the ray undergo simultaneous elongation. It is evident that in both cases the process must involve the interruption of a considerable number of the parenchymatous cell-series of the ray, and we have already seen that this actually occurs.

Before leaving the subject of the principal medullary rays, something must be said of their modified structure in the infranodal region. Such a ray almost always broadens out just below the node, forming, as seen in tangential section, the "lenticular organ" of previous memoirs.† In this region the cells of the ray are very numerous, and generally isodiametric throughout, often contrasting sharply with the more elongated elements in the rest of the ray (see Plate 72, photographs 5 and 6). The cells toward the middle of the infranodal tissue of the ray are generally smaller, and frequently have thicker walls than their neighbours. The most careful investigation, however, has failed to reveal any traces of vascular tissue in this position. The preservation of the specimens is often so perfect, that such tissue, if it had been

* See KNY, "Zur Kenntniss der Tracheiden," 'Ber. d. Deutsch. Bot. Gesellschaft,' vol. 4, 1886.

† WILLIAMSON, "Organization," Part IX., p. 326.

present, could not have been overlooked.* The infranodal portion of the ray is persistently parenchymatous throughout the whole thickness of the secondary wood, and scarcely ever contains any interpolated tracheides. Hence, in tangential sections through the outer wood, where the principal rays generally are obliterated by interfascicular wood, the lenticular masses of parenchyma below each node form a most conspicuous feature (see photograph 6, also WILLIAMSON, "Organization," Part IX., Plate 20, fig. 24). Somewhat similar persistent tracts of parenchyma are sometimes found immediately *above* the node, but they are on a much smaller scale.

It very frequently happens that the infranodal tissue of the principal rays undergoes disorganization of its inner cells, leading to the formation of the radial *infranodal canals*, so fully discussed in previous memoirs.† It is well known that these infranodal canals afford the explanation of those protrusions on the medullary casts, which are placed immediately below the nodes, and between the furrows corresponding to the bundles (see the photographs in Plate 86). This explanation has been accepted by Count SOLMS-LAUBACH,‡ and indeed admits of no doubt, if, for example, we compare the wonderfully preserved cast figured in a former paper,§ with such a tangential section as that shown in our photograph 6. The agreement between the radiating, spoke-like rods of the cast, and the infranodal rays, as shown in the sections, is exact, not only as regards position, but also in size and sectional form.

The extent to which the disorganization of the infranodal parenchyma took place *during life* may well have varied in different specimens. In any case it would have perished during fossilization much sooner than the woody tissue surrounding it, and this is quite enough to account for the marks on the casts.

THE SECONDARY CORTICAL TISSUES.

It is extremely rare to find the cortex of the older specimens in any degree preserved. Except in the comparatively young stems already discussed, all the tissue from the cambium outwards has usually disappeared. The only instance of a really large corticated stem, with which we are acquainted, is that described in a former memoir,‖ and already referred to above.

Here the zone of cortex preserved is even broader than the wood, and measures $2\frac{1}{4}$ inches in thickness. The preservation is very imperfect, but in the radial section (C.N. 80) it is possible to distinguish at least two zones of elongated, square-ended cells, with a regular radial arrangement. We cannot doubt that this tissue was of

* As in C.N. 20B, 138*, and others, besides those photographed.

† WILLIAMSON, "Organization," Parts I. and IX. As regards the true Calamitean stem (as distinguished from that of *Calamopitus*), these canals are especially well shown in C.N. 24, 91, 138*, and 1943.

‡ *Loc. cit.*, p. 312.

§ WILLIAMSON, "Organization," Part IX., Plate 21, fig. 31.

‖ WILLIAMSON, "Organization," Part IX., Plate 20, figs. 14–21. The sections are C.N. 79–87.

the nature of internal periderm. In other parts the cortex consists of prosenchymatous cells.

A specimen of a comparatively small stem, which we have recently examined, throws great light on the origin of the periderm from the primary cortical tissues (see Plate 79, fig. 18). The transverse section shows that the cortex is well-preserved throughout, though in most places somewhat separated from the wood by the intrusion of rootlets of *Stigmaria*. Many of the large parenchymatous cells of the cortex are divided up by tangential septa into short radial series. The divisions are not limited strictly to any one zone of the cortical tissue, but occur chiefly in its inner portion, through which a fairly regular band of dividing cells can be traced. We think that there can be no doubt that we have here to do with an early stage of the formation of periderm. It is certain that a secondary tissue of some kind is being formed by the division of cortical cells. We know, from the older specimen, that internal periderm was formed abundantly in the cortex; we can scarcely be wrong in correlating the two facts.

It may be worth while to state expressly that the specimen from which fig. 18 is drawn has the whole thickness of the wood perfectly preserved, and is a typical *Calamites*, such as that shown in Plate 72, photograph 3.

THE DIAPHRAGMS.

Before leaving the subject of secondary changes in the stem of *Calamites*, we wish to call attention to the formation of periderm on the diaphragms. These persistent plates of parenchyma, which separate the internodal cavities of *Calamites* from one another, have often been described.* When well preserved it is always evident that they are several cells in thickness. The inner layers of cells of the diaphragm often have thicker walls than those towards the upper and lower surfaces. We have often observed that the thin-walled superficial cells are divided up by cell walls parallel to the surface. In some specimens these divisions have taken place so freely that a layer of regular periderm-like tissue coats the diaphragm on either side (see Plate 79, fig. 19). It is most probable that this secondary tissue really represents a layer of internal cork, which isolated the persistent diaphragm from the disorganizing tissue, by the destruction of which the medulla became fistular.

Analogies are not wanting, among recent plants, for the formation of periderm in the pith. It occurs, for example, in certain anomalous Campanulaceæ and Gentianeæ, and in *Aconitum*.† In *Calamites*, however, so far as we have observed, the medullary periderm seems to be limited to the surface of the diaphragms, and not to extend to the peripheral layer of persistent pith which surrounds the medullary cavity.

* See WILLIAMSON, "Organization," Parts I. and IX.

† See JOST, 'Bot. Zeitung,' 1890, pp. 443 and 491; HÉRAIL, "Recherches sur l'Anatomie comparée de la tige des Dicotylédones," 'Ann. Sci. Nat., Bot.,' series 7, vol. 2, 1885.

The Branching of Calamites.

Many of the specimens investigated show the insertion of lateral branches upon a relatively main axis.* In the great majority of these instances the branches are of small diameter compared with the stem which bears them. In judging of the relative dimensions, however, caution is necessary, for we know that in many cases the pith of the branch tapered almost to a point towards its insertion, giving rise to the well-known conical terminations of many of the medullary casts (see the figures in Plate 86). But, making due allowance for this fact, there can still be no doubt of the relatively small size of the lateral branches in very many cases, especially in those where several were given off at the same node. As already stated, the branches are always inserted immediately above a node, and are nearly always placed between two of the outgoing foliar bundles (see Plate 72, photographs 5 and 6; Plate 80, fig. 21; also WILLIAMSON, "Organization," Part IX., Plate 21, fig. 28, where *m* indicates the foliar bundles).† An exception is presented in a section of *Calamopitus*, in which a branch appears to be inserted immediately above one of the bundles,‡ and in one case, so far as we have observed, in the typical *Calamites*.§

The branches often have a verticillate arrangement, but do not seem to have been disposed in the whorl with any great regularity. Thus the transverse sections of one of the largest stems showing structure,‖ pass through four lateral branches at the same node, which are placed at irregular intervals. Sometimes a single branch only was developed at a node, as is very clearly shown in the specimen¶ from which fig. 20, on Plate 79, is drawn. On the other hand a tangential section of a large stem shows four branches, regularly arranged at the same node, and suggests that here the whorl (of which such a section can only show a small part) may have been complete. Two of the four branches are shown in photograph 5, on Plate 72.

The structure of the branch at or near its insertion is very clearly shown in a number of preparations (see Plate 72, photographs 5 and 6; Plate 79, fig. 20; Plate 80, figs. 21 and 22). Tangential sections through the inner part of the wood of the main stem show the basal portion of the branch in transverse section. In such preparations** we see that the branch has a parenchymatous pith, often completely preserved, sometimes partly fistular. Surrounding the pith we find a ring of xylem, arranged in more or less distinct bundles, which, though less obvious than those of an ordinary free stem, are still quite indubitable in good sections. That in these bundles

* See the descriptions and figures in former Memoirs; WILLIAMSON, "Organization," Parts I. and IX.

† Also well shown in C.N. 20B, 90, 138*, &c.

‡ See WILLIAMSON, "Organization," Part I., Plate 28, fig. 38.

§ C.N. 1937.

‖ C.N. 133*, 134*, &c. From 134* the fig. 22 on Plate 80 is taken.

¶ C.N. 132**.

** As in C.N. 20B, 90, 138*, besides those figured; see also WILLIAMSON, "Organization," Part IX., Plate 21, fig. 28.

we really have the primary wood of the branch, is conclusively proved by sections which are transverse to the main stem, and pass tangentially through the base of the branch (see Plate 79, fig. 20).* Here we see the bundles of the branch in longitudinal section, with their annular and spiral tracheæ, and the bands of interfascicular parenchyma between them. In the tangential sections of the main stem (transverse to the branch) it is also easy to demonstrate the elements of the primary xylem of the branch, when they are cut at all obliquely. Our best example of this is the section shown in Plate 80, fig. 21, which passes close to the pith of the parent stem, and therefore shows the branch at its actual base. Here the groups of primary xylem around the pith of the branch are perfectly obvious, and we can distinguish their spiral tracheæ. On the lower side of the branch we can directly trace the continuity of its primary xylem with the nodal wood of the main axis.

The characteristic internodal canals of the Calamitean stem are not present at the actual base of the branch (see photograph 9 on Plate 73, and fig. 21 on Plate 80). Neither are they found, in their typical form, in any part of the branch, so far as it is embedded in the wood of the main axis. In sections which pass transversely through the branch, at any point beyond its actual inner extremity, we frequently find a ring of gaps in its tissue (not to be confused with accidental lesions), situated immediately within the xylem-bundles (see Plate 72, photograph 5, and more especially photograph 6). These gaps are less regular in form than the normal canals, and also differ from them in a more important point, for, as a rule, they are not empty, but are occupied by a lax tissue, consisting of rather large and thin-walled cells. Within the gap, among the thin-walled cells, we can often detect the protoxylem elements of the primary bundle.† Hence we regard these gaps as corresponding to the typical canals of an ordinary stem, in so far as they mark the position of the disorganized protoxylem-groups. As to the lax tissue which usually fills these spaces, two views are possible. It may have been primary, consisting of parenchymatous cells which were present among the primitive tracheæ from their first origin; or it may have been a new formation, analogous to a thylosis, such as has been observed in the carinal canals of *Equisetum*.‡ We regard the latter view as the more probable. All our specimens showing branching are comparatively advanced stems, with a considerable thickness of secondary wood. Hence it is almost certain that the primary tissue at the base of the branch would have already become functionless, especially since many of these branches were evidently abortive, as will be shown below. The formation of thyloses under such conditions is quite probable. We are the more inclined to this hypothesis from the fact that the tissue filling the gaps is conspicuously different from the sur-

* The same point is shown in a similar section of another specimen, C.N. 132*. In one of the preparations kindly lent to us by Count SOLMS-LAUBACH, this structure is, if possible, even more beautifully preserved than in the section figured.

† As in C.N. 20B, and 1554.

‡ See STRASBURGER, 'Histologische Beiträge,' 3, p. 437.

rounding parenchyma. A similar filling of the canals with parenchyma has once or twice been observed in the ordinary free stems.

The primary xylem-bundles of the branch are usually surrounded on the outside by a zone of radially-arranged secondary wood, no doubt the product of the cambium of the branch. In fig. 21 we see that secondary wood has only been formed towards the upper side of the branch. On the lower side the primary wood was continuous with that of the stem, and so no cambium could be formed. Further towards the exterior this hindrance no longer exists, and the zone of secondary wood becomes complete (see photographs 5 and 6, Plate 72).

The secondary wood of the branch is connected in the most complete manner with that of the main stem on which it is inserted. The direct connection is mainly from below. Here the secondary tracheides of the parent axis abut immediately on those of the branch. Other tracheides pass up from below, at the sides of the branch, and bend over to join its lateral strands of xylem, while others again curve round over the top, and bend down to form a union with the wood on the upper side of the branch. The whole structure bears a most striking resemblance to the insertion of a lateral shoot of *Pinus*, as figured, in tangential section, by Professor STRASBURGER.* Occasionally, a few tracheides appear to be continuous in the upward direction, from the branch into the wood.

A radial section through the insertion of a branch, figured in a previous memoir,† shows with great clearness how the pith of the branch terminates inwards in a narrow neck, by which it is continuous with the pith of the parent stem. The same fact is shown in various transverse sections (see Plate 79, fig. 20, which, however, is not *median* through the branch; and Plate 80, fig. 22). The series of transverse sections cut from the base of the specimen discovered by Mr. WILD, and already referred to, also illustrates the point (see Plate 73, photographs 7, 8, and 9). At a distance from its base the branch has a large fistular pith, surrounded by a ring of about 24 bundles, of the normal structure (photograph 7). Lower down the pith is much smaller; the bundles are still normal, but are much reduced in number (photograph 8, which shows 14 bundles). At the base itself the pith is reduced to a minute body, and is no longer fistular. The vascular bundles are not more than 10 in number, are crowded closely together, and their canals can no longer be recognized (photogragh 9). In fact, we have here almost reached the inner termination of the branch, such as is shown, in connection with the main axis, in Plate 80, fig. 21. All these facts agree exactly with the appearances presented by the medullary casts (see Plate 86).

So far as we have gone, the structure of the branches in their basal regions has been sufficiently intelligible. Certain difficulties, however, remain. If we examine tangential sections through the outer layers of the secondary wood, and passing

* 'Histologische Beiträge,' vol. 3, plate 2, fig. 40.

† WILLIAMSON, "Organization," Part IX., Plate 21, fig. 27 (C.N. 97).

transversely across a branch at some little distance from its actual base, we often find a highly peculiar structure, already described and figured in former memoirs.* The transverse section of the branch shows no well-defined pith and no clear traces of the primary groups of xylem. It consists of a parenchymatous mass, into which tracheides penetrate in all directions from the surrounding secondary wood. These intruding tracheides describe strange curves, and extend as far as the middle of the branch, cutting up the parenchyma into isolated groups.† In fact, in these cases, as we trace the branch outwards, its structure, instead of approaching more nearly to that of the normal Calamitean stem, becomes more and more anomalous. Such a structure is in fact totally different from that of a *Calamites* or any other known stem. From the sections of Mr. WILD's specimen we know that no such peculiarities are found in a normal branch, at any point, from its base upwards. We believe that the true explanation is to be sought in the fact that the remarkable structure in question is not a normal one, but is due to the abortion of the branch, and the consequent enclosure of its base by the secondary wood of the parent stem.

We have direct evidence proving that branches became abortive and were enclosed by the wood. A good illustration of this is afforded by the radial section already mentioned.‡ Here the normal pith of the branch can be traced outwards, up to a certain point, at which it is suddenly cut off by a layer of secondary wood seen in radial section. The section is obviously median, so there can be no doubt that the wood really shuts off the end of the truncated branch. Precisely the same phenomenon is shown in some of the transverse sections (see Plate 80, fig. 22), which pass through the median plane of a branch. Here also the parenchymatous pith of the branch extends for a certain distance from the base, and is then suddenly cut off by a mass of secondary wood, which, in this case, is seen in transverse section. The line between the pith of the branch and this callus-wood, if we may call it so, is nearly straight, or if anything convex towards the interior, so the appearances cannot possibly be explained by obliquity of section. We have, in fact, two other sections of the same branch, passing one above, the other below, its median plane, and the three together prove conclusively that the truncated end is completely shut in by secondary wood.§

In these, and other similar cases, it is evident that a meristem was formed across the pith of the branch, at a certain stage, by which secondary wood was formed, completely cutting off the basal portion of the branch from all direct communication with the exterior. We can hardly doubt that the free end of the branch was previously or simultaneously cast off. It is impossible to say at what stage of

* See WILLIAMSON, "Organization," Part IX., Plate 21, fig. 26.

† As shown in C.N. 88, 131*, and other preparations.

‡ C.N. 97, WILLIAMSON, "Organization," Part IX., Plate 21, fig. 27.

§ The sections in question are C.N. 133*, 134*, and 135*. From the middle one our figure is drawn. Other branches in the same preparations show the same structure.

development of the branch abortion took place. Possibly it never advanced much beyond the condition of a bud, more probably it formed a shoot of limited duration, comparable to the short leaf-bearing shoots of *Pinus*.

This then we believe to be the explanation of the apparent intrusion of tracheides into the middle of the branch. The tracheides which appear to penetrate into the branch, represent, in our opinion, the commencement of that formation of callus-like wood, by which the base of the lateral shoot soon became completely enclosed.

We have gained, then, this additional fact respecting the branches of *Calamites:* in many cases they were abortive, or of short duration, and their bases then became shut in, like "knots," by the wood of the parent stem.

One specimen, previously figured,* shows a branch somewhat different from those already described. The stem and branch are enclosed within a common zone of secondary wood, and the sections show that the dimensions of the two are approximately equal, as is also the number of their vascular bundles. Evidently we have here to do with a different order of branching from that which we have just considered. In this specimen the branch repeats the characters of the main stem, and was presumably of equal morphological importance ; in the previous cases the branches were relatively small lateral appendages, and probably of limited duration.

As regards the mode of origin of the branches, we are necessarily without any direct evidence. Now, however, that the continuity between the primary tissues of the branch and those of the main stem has been demonstrated, there can be no doubt that the ramification took place while the axis was still young. In fact we have every reason to suppose that the branching was normal, not adventitious, and that the lateral shoots arose, like the normal branches of *Equisetum* or any other vascular plant, in the immediate neighbourhood of the growing point. The secondary wood in which the base of the branch is imbedded, was evidently deposited after the branch had been formed ; the stem and branch together became invested simultaneously by a common woody zone. In fact the conditions in *Calamites* are the same as in the branching of any stem with secondary growth in thickness, and present no special difficulties, now that the facts are known.

The successive changes in structure which we find in a branch, as we trace it from its base upwards, have already been described. The changes consist essentially in a rapid increase in the diameter of the pith, and in the number of vascular bundles surrounding it.

These facts, which have been already demonstrated by the study of specimens showing structure, are exactly reproduced in those medullary casts which represent the pith-cavity of lateral branches. After the fundamental truth had been established, that the sandstone and other allied specimens, which were long believed to be the actual stems of *Calamites*, were merely inorganic casts of a central cavity from which

* WILLIAMSON, "Organization," Part IX., Plate 21, fig. 31, A and B (C.N. 102).

the medullary tissue had disappeared,* the study of these plants underwent a radical change. The idea that the base of a large lateral branch adhered to the stem solely by a minute constricted neck, having been shown to be an impossible thing,† search had to be made for the true sustaining structures, and these were found in the strong zone of secondary xylem.

The following series of photographs, taken from seven specimens of medullary casts, preserved in the Natural History Department of the British Museum, illustrate the structure of the branch, from its base upwards. Such casts, when perfect, invariably terminate at their lower extremity in a very narrow conical point, on which no traces of the vertical grooves and ribs, indicating the number and position of the vascular bundles, and the primary rays, are present. This point corresponds to what, in the following tables, is designated the *proto-medulla* of the branch, *i.e.*, the basal portion of its pith by which it was connected with that of the parent stem.

These tables give the length and circumference of each internode, as well as the number of its woody wedges (vascular bundles); in all these respects an increase takes place in each successively higher internode, for a limited distance, as we ascend. Beyond the point where this increase is checked, which is usually within a few inches from the conical base of the pith of the branch, the latter is prolonged to a more or less considerable height, with very little further change in the features referred to. This fact was remarkably illustrated by the medullary cast of a stem, discovered by Mr. GEORGE WILD in the roof of a colliery under his superintendence near Ashton-under-Lyne. This specimen, which was a portion of the middle part of a Calamite, was 30 feet in length, but while the diameter of the pith at its lower end was 11·5 centims., at its upper extremity it had only increased to 15·2 centims., a very small increase in a stem of such a length.

The photographs represent (with the exception of F) the basal portions of the specimens, and the accompanying tables give the measurements and number of vascular bundles in each internode, as above explained.

* WILLIAMSON, "Organization," Part I., 1871.

† WILLIAMSON, "Organization," Part IX.; see Plate 21, fig. 30.

TABLES and Photographs from Medullary Casts.

Specimen A.

Column I. Number of internode.	Column II. Vertical length of internode.	Column III. Circumference of internode.	Column IV. Number of vascular bundles in circumference of internode.
7	Imperfect		43
6	4·1 centims.		39
5	1·8 ,,		31
4	1·3 ,,		22
3	1·0 centim.		16
2	0·4 ,,		11
1	0·35 ,,		Not distinct
	Proto-medulla	almost destroyed.	

See Photograph A, Plate 86.

Specimen B.

Column I. Number of internode.	Column II. Vertical length of internode.	Column III. Circumference of internode.	Column IV. Number of vascular bundles in circumference of internode.
7	3·0 centims.	8·0 centims.	61
6	2·0 ,,	8·0 ,,	55
5	1·5 ,,	8·5 ,,	49
4	1·1 ,,	8·6 ,,	45
3	1·4 ,,	8·1 ,,	46
2	1·0 centim.	6·2 ,,	35
1	0·65 ,,	5·0 ,,	27
Basal portion*	0·70 ,,		

See Photograph B, Plate 86.

* Upper half with ill-defined traces of bundles; lower half proto-medulla of branch.

Specimen C.

Column I. Number of internode.	Column II. Vertical length of internode.	Column III. Circumference of internode.	Column IV. Number of vascular bundles in circumference of internode.
10	6·0 centims.	8·5 centims.	36
9	4·5 ,,	Imperfect	Imperfect
8	4·5 ,,	8·5 centims.	31
7	2·5 ,,	8·3 ,,	29
6	1·5 ,,	8·0 ,,	24
5	1·0 centim.	7·6 ,,	20
4	1·0 ,,	6·5 ,,	15
3	0·4 ,,	5·5 ,,	12
2	0·3 ,,	4·8 ,,	6 or 7
1	0·3 ,,	3·2 ,,	5 or 6
Proto-medulla . . .	..	1·1 ,, at its upper portion	

See Photograph C, Plate 86.

Specimen D.

Column I. Number of internode.	Column II. Vertical length of internode.	Column III. Circumference of internode.	Column IV. Number of vascular bundles in circumference of internode.
9	3·8 centims.	9·0 centims.	50
8	3·1 ,,	8·3 ,,	49
7	2·5 ,,	7·7 ,,	40
6	2·2 ,,	7·7 ,,	41
5	1·5 ,,	7·5 ,,	35
4	1·1 ,,	5·1 ,,	32
3	0·7 centim.	3·7 ,,	23
2	0·5 ,,	3·1 ,,	14
1	Imperfect	Imperfect	Imperfect

See Photograph D, Plate 86.

Specimen E.

Column I. Number of internode.	Column II. Vertical length of internode.	Column III. Circumference of internode.	Column IV. Number of vascular bundles in circumference of internode.
11	1·9 centim.	23·5 centims.	38
10	1·4 ,,	All lower internodes	32
9	1·3 ,,	more or less com-	30
8	1·3 ,,	pressed	26 or 27
7	1·1 ,,		25
6	1·0 centim.		23
5	0·8 ,,		19
4	1·0 ,,		20
3	0·8 ,,		About 18
2	0·8 ,,		13
1	Partly disorganized		Some well-formed, but partly disorganized and broken away

See Photograph E, Plate 86.

Specimen F.

Column I. Number of internode.	Column II. Maximum vertical length of internode.	Column III. Semi-circumference of internode.	Column IV. Number of vascular bundles in semi-circumference of internode.
5	6·0 centims.	15·2 centims.	about 50
4	5·5 ,,	15·3 ,,	53
3	5·5 ,,	15·5 ,,	53
2	5·5 ,,	15·5 ,,	54
1	4·0 ,,	15·5 ,,	54

This specimen is from a part of a branch some distance above its base, and consequently the dimensions are fairly uniform throughout.

See Photograph F, Plate 86.

Specimen G.

Column I. Number of internode.	Column II. Vertical length of internode.	Column III. Circumference of internode.	Column IV. Number of vascular bundles in circumference of internode.
10	4·0 centims.	9·2 centims.	33
9	3·4 „	9·5 „	34
8	3·0 „	9·0 „	28
7	2·1 „	9·0 „	23
6	1·6 „	8·6 „	19
5	1·3 „	8·1 „	18
4	0·85 centim.	8·0 „	18
3	0·65 „	7·3 „	about 14
2	0·60 „	6·5 „	„ 12
1	0·50 „	4·8 „	„ 10, but indistinct
Basal portion without distinct bundles, but probably too large for protomedulla			

See Photograph G, Plate 86.

The Roots of Calamites.

When we began writing the present paper we did not expect to be able to throw any light on the structure of the root of *Calamites.* Specimens showing the roots in connection with the stems, and having at the same time the internal structure preserved, were not yet known to us. Consequently it was impossible to determine which, if any, of the petrified remains were to be assigned, as roots, to the Calamitean stems.

One of us, however (D. H. Scott) has recently had the opportunity, through the kindness of M. Renault, of examining certain specimens in his collection, which place the question in quite a different light. Two of these specimens show an axis, with the structure of *Astromyelon,* in actual continuity with the stem of an Arthropitoid Calamite, identical with such as we have described in this paper. Hence the opinion which M. Renault first expressed in 1885,* is confirmed in a most striking manner. There can be no doubt, from the evidence of these specimens, that the *Astromyelon* in question is an appendage of the stem of *Calamites* (Arthropitys of the French authors). Whether this appendage is to be regarded as morphologically a *root,* is another question, but the anatomy renders it highly probable that this is its true nature.

Yet another question remained ; are the English specimens on which the genus

* "Nouvelles Recherches sur le genre *Astromyelon,*" 'Mém. de la Soc. des Sci. Nat. de Saône et Loire,' 1885.

Astromyelon was founded identical with the Calamitean appendages of M. RENAULT's collection?

We propose to reserve the detailed consideration of *Astromyelon* for another occasion, but a preliminary examination of the slides in the WILLIAMSON Collection shows that the larger specimens, at any rate, namely those with a distinct pith,* have the same structure as M. RENAULT's specimens, which are directly borne on a Calamitean stem. The question as to the identity of *all* the forms grouped under *Astromyelon* in a former memoir,† will have to be reconsidered in the new light which has now been thrown on these fossils. It is, however, highly probable that we possess, in the various forms of *Astromyelon*, not merely the principal roots, but also the finer rootlets of *Calamites*.

It is interesting to recall the fact that the first specimens of *Astromyelon* were originally described under the name of *Calamites*,‡ but subsequently separated, on the ground of certain structural differences which find a sufficient explanation, if the organs in question are to be regarded as roots and not stems.§

We still require much further information respecting the earliest stages of the development of *Calamites*, in order to fill up the gap between two states, as to which we already possess considerable knowledge. We now know the spores of *Calamites pedunculatus*‖ which we may regard as a typical fructification of the Arthropitoid Calamites, and which appears to have been homosporous. We also know that at a later stage the true *Calamites* sprang from rhizomes, with normal nodes and internodes, which were very slender, as compared with the typical stems. We are indebted especially to M. GRAND'EURY for this information.¶ He figures, among many other specimens, one of these rhizomes, which gives off from several points stems of the normal Calamitean type. These stems, though merely preserved as sandstone medullary casts, devoid of all traces of xylem or cortex, are many times larger than the rhizome from which they spring. We unfortunately know nothing of the organization of these rhizomes. If their structure should turn out to be simpler than that of the normal stem of *Calamites*, we may find in them an early stage of development of the plant.

We cannot doubt that *Calamites*, like the *Equiseta*, and all recent Vascular Cryptogams, possessed a sexual prothallus, though its discovery is doubtless impossible. We may conjecture that the first product of the prothallus after fertilization may have

* Such as that figured in WILLIAMSON, "Organization," Part XII., Plate 27, fig. 3.

† *Loc. cit.*, Part XII.

‡ WILLIAMSON, "Organization," Part I., Plate 25, fig. 16.

§ WILLIAMSON, *loc. cit.*, Part IX., p. 319.

‖ The name which we propose to give to the strobilus described by WILLIAMSON, in "Organization," Part XIV. See below, p. 916.

¶ 'Flore Carbonifère du Département de la Loire, &c.,' 1877.

been of the nature of a rhizome. If so, the latter forms an important link in the life-history leading from the spore to the typical plant.

II. CALAMOSTACHYS.

The following observations relate to three forms belonging to this genus :

1. *Calamostachys Binneyana*, SCHPR. (homosporous).
2. *C. Casheana*, WILLIAMSON (heterosporous).
3. A doubtful form, which may, however, *possibly* be referable to *C. Casheana*.

Calamostachys Binneyana, which we will first consider, is one of the best-known of the fructifications found in the Coal-Measures,* and we are now in a position to describe almost every detail of its structure. Unfortunately, however, the specimens before us afford no direct evidence whatever as to the nature of the stem on which the fructification was borne. In no case has *C. Binneyana* been found in connection with vegetative organs of any kind. In endeavouring to determine to what kind of plant the strobilus belonged, we can, therefore, only be guided (1) by the morphology and anatomy of the strobilus itself, and (2) by the specimens in which similar, though not identical fructifications have been found in actual connection with the stems which bore them. Many such specimens have been described and figured by WEISS and other authors,† and they leave no doubt that fructifications of the *Calamostachys* type belonged to plants of the family Calamarieæ. The whole question, however, can only be profitably discussed after the structure of *Calamostachys* has been described in detail.

CALAMOSTACHYS BINNEYANA.

1. *General Morphology.*

The specimens available for examination consist solely of strobili or portions of strobili ; not even a peduncle is found in connection with the fructifications, and its constant absence leads us to suppose that the fruit was a sessile one.

The largest strobilus known to us measures $1\frac{3}{8}$ inches (3·4 centims.) in length, and is probably not an absolutely complete specimen. The photographs 10 and 11 on Plate 73,

* See, for example, BINNEY, "Observations on the structure of Fossil Plants foundin the Carboniferous strata (*Calamodendron commune*)," 'Palæontographical Society,' 1867; CARRUTHERS, "On the structure of the fruit of *Calamites*," 'SEEMANN'S Journal of Botany,' vol. 5, 1867; WILLIAMSON, "Organization," Part V., 1873; Part X., 1880; Part XV., 1889; WEISS, "Steinkohlen-Calamarien," I., 1876, and II., 1884. STUR, 'Calamarien der Schatzlarer Schichten.'

† WEISS, *loc. cit.*, Parts I. and II. See especially the closely allied *C. Ludwigi*, Part II., 'Atlas,' Plate 18, fig.2. WILLIAMSON, "Organization," Part V., Plate 5, fig. 32. RENAULT, 'Cours de Botanique Fossile,' vol. 2, &c.

represent portions of this strobilus. The maximum diameter is about 7·5 millims. Most of the specimens are considerably smaller.

The fructification consists of a rather slender axis, bearing numerous whorls of appendages, which are of two kinds, fertile and sterile. The former will be spoken of as *sporangiophores*, the latter as *bracts*. The sterile and fertile verticils succeed one another in regular alternation. Above each whorl of bracts is one of sporangiophores, then another of bracts, and so on (see Plate 73, photographs 10 and 11).

The whorls are equidistant from one another, each fertile whorl being placed exactly in the middle of the internode between two verticils of sterile bracts. This character at once sharply distinguishes the *Calamostachys* type of fruit from the Calamitean strobilus described in previous papers,* and from the forms described by WEISS,† under the name of *Palæostachya*, in both of which the sporangiophores arise from the angle between the sterile whorl and the internode above. In the large cone already mentioned (see photographs 10 and 11) eighteen whorls of bracts were present, with the corresponding whorls of sporangiophores between them. The total number in the strobilus, when complete, was probably somewhat greater.

Each sterile whorl consisted of about twelve‡ coherent bracts, forming a horizontal disc, at the margin of which the bracts became separate from one another, and bent sharply upwards, extending at least as far as the second sterile whorl above (see photograph 10). Consequently any transverse section of the strobilus passes through at least two alternating series of these overlapping extremities of the bracts. It follows that each fertile verticil is enclosed by a ring of free bracts belonging to the two sterile whorls below (see Plate 73, photographs 12 and 13 ; Plate 74, photograph 14).

The bracts of successive sterile whorls, as already indicated, alternate with one another, so that the free extremities of the bracts of any verticil pass between those of the verticil next above. This is easily seen in tranverse sections of the strobilus, such as those shown in the photographs just referred to. The fact is also evident from the tangential sections, in which the distribution of the vascular bundles in the coherent disc affords a useful clue, if the free tips of the bracts cannot be seen (see Plate 73, photograph 11).

The cohesion of the bracts serves to distinguish *C. Binneyana* from the very similar *C. Ludwigi*, CARR., in which they are free throughout almost their whole extent.§

The fertile whorls consist of the sporangiophores, a name which we prefer to

* WILLIAMSON, "On a new form of Calamitean strobilus, &c.," 'Mem. Lit. and Phil. Soc. of Manchester,' Series 3, vol. 4, 1870; "Organization," Part XIV.

† 'Steinkohlen-Calamarien,' Part I., 1876, Plate 15, and Part II., 1884, Plate 16, fig. 2; Plate 21, fig. 4; Plate 22, fig. 15. See also RENAULT'S *Volkmannia gracilis*, 'Ann. des. Sci. Nat., Bot.' Sér. 6, vol. 3, Plate 2, 1876.

‡ There were thirteen in C. N. 997, from which the Photograph 12, on Plate 73, was taken.

§ See WEISS, *loc. cit.*, Part 2, 'Atlas,' Plate 22, fig. 8.

sporophylls, as the morphological nature of these organs is somewhat doubtful, in view of their remarkable variations in position, in various Calamarian fructifications.

The sporangiophores in each verticil are usually about half as numerous as the bracts of a sterile whorl (see Plate 73, photograph 13). We have found 6, 7, and 8 in different whorls, and the number seems to have varied even in the same specimen. Six seems to be the most frequent number. It is evident that the sporangiophores cannot always have been exactly half as numerous as the bracts, for the number of the latter may be uneven (see photograph 12 on Plate 73), nor have we seen any sterile whorl with as many as 16 bracts.

The sporangiophores, unlike the bracts, do not alternate with one another in successive whorls, but are placed one above the other, in vertical rows (see Plate 73, photograph 11). Hence, it is evident that their position can bear no constant relation to that of the bracts.

Each sporangiophore consists of a stalk or pedicel, having a peltate expansion at its free end. The pedicel is broadest at its base (see Plate 73, photograph 13, and Plate 81, fig. 29).

The peltate expansion of the sporangiophore bears four sporangia, which are attached to its underside, at the extreme edge. A tangential section of the strobilus constantly shows the four diagonally placed sporangia grouped around the pedicel of each sporangiophore (see Plate 73, photograph 11, Plate 81, fig. 30).

The whorl of sporangiophores, with their sporangia, appears to have almost filled up the space between two successive verticils of bracts.

The short sketch which we have given of the general morphology of the strobilus is sufficient to show that, so far as the sporangiophores are concerned, *Calamostachys* shows a general resemblance to *Equisetum*, as has often been pointed out before. The smaller number of sporangia on each "peltate scale" is not a difference of much importance.

The alternating verticils of sterile bracts are, however, without an analogue in *Equisetum*, unless indeed we regard the "annulus" in the latter genus as representing a single whorl of bracts at the base of the strobilus. It is evident that *Calamostachys*, and indeed all the allied fructifications, were more highly differentiated than those of existing *Equiseta*.

We will now proceed to consider the structure of *C. Binneyana* in detail, beginning with that of the axis.

2.—*Structure of the Axis.*

The axis of the strobilus is in all cases traversed by a central cylinder, or *stele*,* which consists of a pith, surrounded by a ring of vascular bundles. Two distinct

* We adopt the convenient term, introduced by M. VAN TIEGHEM, for the whole central cylinder, whether of a root or stem, including pith (if present), vascular bundles, interfascicular tissue, and

types of stele are present in different specimens. The one, as seen in transverse section, has a bluntly triangular form, with the vascular bundles situated at the prominent corners (see Plate 80, figs. 23 and 24). In the other type, the stele is approximately quadrangular, with a bundle at each angle (see Plate 74, photograph 14; and Plate 80, fig. 25). In the specimen photographed the angles are especially prominent, and the sides concave, so that the whole section of the stele is somewhat cruciform. The triangular and quadrangular types are quite distinct. The difference between them does not depend on the level at which the transverse section is taken; for we find the two structures indiscriminately in sections passing through the sterile node, the fertile node, or an intermediate internode. On the whole the triangular form is the more frequent of the two. We found the quadrangular form of stele only in cases where the number of sporangiophores in a verticil is 8; the converse, however, does not hold good, for in one preparation showing eight sporangiophores, the stele is distinctly of the bluntly triangular type.*

We will describe this type first. The whole middle portion of the cylinder, forming much the greater part of its mass, so far as primary structure is concerned, consists of the pith. The whole of the pith appears to have been persistent; sometimes a few cells near the centre have disappeared (Plate 80, fig. 23), but this is obviously due to imperfect preservation. In many cases the outer zone of medullary cells has thickened walls, while those nearer the middle are more delicate (Plate 80, figs. 23 and 24). In other specimens the entire pith is thick-walled throughout.†

It is often difficult or even impossible to distinguish the thick-walled medullary cells from tracheides, in a transverse section. From this difficulty the mistake arose of regarding the stele of *Calamostachys* as a solid vascular axis, a mistake which was corrected in a previous memoir published in 1889.‡

Longitudinal sections show that the cells of the pith are elongated and often prosenchymatous, especially those towards the periphery (see Plate 81, fig. 27).

The vascular bundles are placed at the projecting angles of the triquetrous stele. It is often difficult to say whether one bundle or two are present at each corner. In some of the clearest sections it is evident that there are two, so that the total number of bundles in the cylinder is, in these cases, six (see Plate 80, figs. 23 and 24).§

At the inner margin of each bundle is an empty space, less definite and regular than an internodal canal in *Calamites*, but constantly present, except at the sterile nodes. These spaces or canals always contain the disorganized remains of spiral or annular tracheides, and evidently mark the position of the protoxylem-group of the

pericycle (see VAN TIEGHEM, "Sur la Polystélie," 'Ann. des Sci. Nat., Bot.,' sér. 7, vol. 3, 1886; and 'Traité de Botanique,' 2nd edition, p. 765.)

* C.N., 1898.

† See WILLIAMSON, "Organization," Part V., Plate 6, fig. 38. (C.N. 989.)

‡ WILLIAMSON, "Organization," Part XV., p. 160; Plate 2, fig. 7.

§ See also the figure in WILLIAMSON, "Organization," Part X., Plate 15, fig. 15.

vascular bundle (see Plate 80, figs. 23 and 24; Plate 81, figs. 27 and 28). Where two distinct spaces are present at each corner of the stele, we are therefore justified in assuming that two distinct vascular bundles existed, as is especially clear in fig. 23. Often however these spaces are not distinct from one another, and it may be impossible to say, in such cases, whether one or two protoxylem-groups were present. We have noticed that the bundles at each corner are most evidently separate at the level of the sporangiophores, as for example in fig. 23. They seem to have diverged a little from one another at the points where the traces of the sporangiophores were given off.

We find then that each prominent angle of the triquetrous stele contains either one vascular bundle, or a pair of bundles in close proximity, the total number of bundles thus being either three or six.*

The amount of primary xylem must have been very small. Some of the preparations show only a single layer of tracheides, to the outside of the protoxylem-gap. In the less perfectly preserved specimens the wood has often broken away altogether, and only the pith is left in position.

The later-formed tracheides were reticulated or scalariform.

Before going further, it will be well to describe shortly the quadrangular type of stele, for much of what remains to be said applies equally to both forms.

In the four-cornered stele the pith shows precisely the same structure as in the type already described (see Plate 80, fig. 25, and Plate 74, photograph 14). At each angle there is a vascular bundle, with a well-marked intercellular space at its inner margin. In this space the remains of the protoxylem-elements can be detected, just as in the previous type. There is no reason to suppose, in this case, that more than one bundle was present at each corner. The somewhat peculiar form of the stele in the beautiful specimen from which Photograph 14 was taken has already been noticed.

The structure of the xylem is identical with that in the triquetrous form.† In the figure referred to in the footnote it will be noticed that the two bundles on the left show no spaces at their internal edge, but are solid strands of tracheides. In the text of the memoir cited,‡ it is pointed out that this part of the section approached a node. As a matter of fact, we have always found, in both types of cylinder, that the intercellular spaces come to an end at the *sterile* nodes, but are continued without interruption through the nodes at which the sporangiophores are borne. This is one of the points in which the sterile, or bract-nodes, of *Calamostachys* resemble the ordinary nodes of *Calamites* (see Plate 81, fig. 28, which shows the structure at a sterile node).

* The structure and arrangement of the vascular bundles are well described, from independent specimens, by Mr. T. HICK, 'Proceedings of the Yorkshire Geological and Polytechnic Society,' vol. 12, 1893.

† See WILLIAMSON, "Organization," Part XV., Plate 2, fig. 7.

‡ *Loc. cit.*, p. 160.

At the bractigerous nodes we also find a girdle of short reticulated tracheides, reproducing, on a small scale, the structure of a typical Calamitean node (see Plate 81, fig. 28, also photograph 10, on Plate 73).

The bundles which pass out to the whorl of bracts leave the cylinder with an obliquely upward course, but soon become perfectly horizontal. These bundles can very seldom be traced through the cortex, for they are usually broken away, in the region where the inner cortical tissue has perished. In one or two cases, however, the continuity is perfect.

The fertile nodes, at which the sporangiophores were inserted, show scarcely any modification of structure, as compared with the internodes. Here the bundles passed out at a right angle, but are very seldom preserved throughout their whole course. The node through which the section shown in Plate 80, fig. 23, was taken, bore seven sporangiophores. It will be noticed that while the stele, as a whole, has an obtusely triangular section, the xylem shows seven small projecting points (*sp.* in the figure). To these were attached the bundles of the seven sporangiophores; the bundle at sp^{+} is partly preserved.

It is not possible to give any regular scheme for the longitudinal course of the leaf-trace bundles in *Calamostachys*, for, as we have seen, the number of bundles in the axis bears no *constant* relation to the number of lateral appendages in a whorl. We may, however, point out that the bundles appear to have passed up the axis in a straight line, and not to have alternated in successive internodes (see Plate 81, fig. 28).

From what has been already said there can be little doubt that the structure of the bundles was collateral. For a long time, however, direct evidence of this was wanting, for in nearly all cases the whole tissue between the wood and the sclerotic outer cortex has perished. In one instance, however, we have found these tissues completely preserved at one side of the axis (see Plate 80, fig. 26). It is highly probable that here the group of small delicate cells, *ph.*, represents the phloëm, while the larger thin-walled cells further to the exterior belong to the inner cortex, or rather perhaps to the pericycle.

In some specimens the primary tissues already described are alone present. Often, however, a well-marked zone of secondary wood is added, as has been fully explained in previous memoirs* (see Plate 80, fig. 24). The secondary xylem is both fascicular and interfascicular; it consists mainly of scalariform tracheæ, with a few parenchymatous rays between them. The radial arrangement of the elements is sufficiently regular to leave no doubt of their origin from a cambium; the secondary wood may attain a thickness of eight or more cells.

In some specimens the growth in thickness had evidently stopped short at a very early stage, when only a few tangential divisions had taken place in the interfascicular

* WILLIAMSON, "Organization," Part V., Plate 10, &c.

tissue (see Plate 74, photograph 14, Plate 80, figs. 23 and 25). Manifestly, the amount of secondary growth in thickness in the axis of the strobilus was relatively small and inconstant, just as we know to be the case in the peduncles of Dicotyledons at the present day. The formation of secondary wood in many cases, however, is amply sufficient to prove that the mode of growth was essentially similar to that of *Calamites.*

The *cortex* of the axis of the strobilus needs no detailed description. Its outer layers, which in most cases are alone preserved, consist of thick-walled elongated cells, often prosenchymatous in form. When portions of the inner cortex are preserved, its cells are similar to those of the more external layers in form, but have thin walls. It is possible that this inner layer should be referred to the pericycle, but we cannot undertake to determine the limits of these tissues with accuracy (see Plate 73, photographs 10–13, Plate 74, photograph 14 ; Plate 81, fig. 27, where only the inner layers are shown).

The epidermis consists of small cells, often with rather thick walls ; we were not able to prove the presence of stomata, but it is quite possible that they existed. The specimens rarely have their epidermis so well preserved as the more internal tissues.

3. *Appendages of the Axis.*

A. *The Bracts.*

The general arrangement of the whorled bracts has been already described. The coherent part of the whorl, or disc, is traversed by vascular bundles equal in number to the free limbs of the bracts, into each of which one of the bundles runs out (see Plate 73, photographs 11 and 12 ; also Plate 81, figs. 30 and 32). As a rule, only the small xylem-strand of the foliar bundle is preserved ; this lies within an empty space, from which the soft tissue has perished. Sometimes a part of this soft tissue is preserved, and then we find it on the *lower* side of the xylem. It thus appears that the bundles were normally collateral, as we should expect.

The mesophyll of the coherent disc usually shows a marked differentiation. Towards the upper surface it consists chiefly of thick-walled sclerenchymatous fibres. Its lower portion is composed of more parenchymatous cells, with wider lumina, and usually thinner walls. Next the lower epidermis we find a small-celled hypodermal layer. The epidermis on both surfaces has small cells, and is seldom very well preserved, so that here also the question of stomata must be left open.

There are many variations in detail in different specimens ; sometimes the whole tissue of the coherent region is comparatively thin-walled (see Plate 81, fig. 30) ; sometimes, on the other hand, the parenchyma, as well as the fibrous tissue, is considerably thickened (see Plate 73, photographs 10 and 11). In some cases a strand of specially thick-walled sclerenchyma follows the course of each vascular bundle on its upper side (photograph 11). Certain large parenchymatous cells towards the

lower surface often contain dense masses of carbonaceous matter, which may represent some secretion formed during life.

As the outer edge of the coherent disc is approached, we find that its upper surface becomes undulated, as seen in tangential section. Each elevation of its surface corresponds to the position of one of the free bracts, which here begin to separate from each other. The free portions of the bracts, as already stated, are of great length. They gradually taper off towards their tips, and their structure undergoes a corresponding simplification.

In its lower region the free part of a bract is composed of the same tissues as are found in the coherent disc, arranged in the same manner. The secretory sacs (if that is their real nature) are especially conspicuous in this part. The upper extremity of the bract consists of sclerenchyma only, through which the fine vascular bundle can be traced for some distance.

The free bracts are shown in longitudinal section in Plate 73, photograph 10, and in transverse section in photographs 12 and 13. In Plate 74, photograph 14, some of them are also shown in oblique superficial view.

It need scarcely be pointed out again that the whole of the highly differentiated bract-system, so characteristic of fossil Calamarian fructifications, has nothing clearly corresponding to it among existing *Equiseta*. In this fact we have a striking illustration of the general rule, that the Palæozoic Cryptogams known to us, were far more highly organized plants than their allies which are living in the present age.

B. *The Sporangiophores.*

The general form of the peltate sporangiophores, and their relation to the axis, have been described above. The pedicel consists of a zone of somewhat sclerotic cortical tissue, enclosing a single vascular bundle (see Plate 73, photographs 11 and 13; Plate 81, figs. 29 and 30). Immediately below the peltate expansion, or head, which terminates the sporangiophore, the pedicel becomes broader, and here the vascular bundle forks into two branches, which lie in the same horizontal plane. Each of the branch-bundles forks again, and the four ultimate ramifications run out to the bases of the four sporangia, which are placed diagonally at the margin of the peltate head (see Plate 81, figs. 29 and 32). The parenchyma of the peltate portion is thin-walled; the free external surface and edges are covered by a very characteristic layer of elongated, palisade-like, epidermal cells. This palisade-layer is very delicate, and is rarely perfectly preserved; it is best shown in a specimen figured in a former memoir* (see also Plate 73, photograph 13; in Plate 81, fig. 29, only fragments of this layer are shown; in the tangential section, Plate 81, fig. 32, the layer is evident).

The general outline of the peltate expansion of the sporangiophore, as seen in

* WILLIAMSON, "Organization," Part XV., Plate 2, fig. 8 (C.N. 1000).

a tangential section of the strobilus, was square, probably somewhat lobed, with depressions between the insertions of the sporangia (Plate 81, fig. 32).

The sporangia were attached to the edge of the peltate head, at its four corners, and on its lower side. Each sporangium is connected with the sporangiophore by a narrow neck of tissue only, through which the vascular bundle passes, to end at the base of the sporangium itself (see Plate 81, fig. 29).* The palisade-layer extends over the short stalk of the sporangium on its outer side, its cells becoming shorter here, and appears to have been continuous with the sporangium-wall.

C. *The Sporangia.*

Each sporangium has the form of a somewhat elongated sac; its long axis is parallel to the pedicel of the sporangiophore, and is therefore radial to the axis of the strobilus. As seen in tangential section the sporangia are approximately square.

In most instances, the sporangium, as preserved in our specimens, has a wall which is one-cell only in thickness. Remains of tissue lining the inside of this persistent layer are frequent, but only show structure in exceptional cases, to be considered presently.

The cells of the sporangial wall are lozenge-shaped, as seen in surface view, their long axes being parallel to the major axis of the sporangium (Plate 81, fig. 31, A). Their lateral walls are thin, but are stiffened by vertical plates, which project, like buttresses, from the cell-wall, and correspond to one another in adjacent cells. These buttresses are broadest at the base, *i.e.*, where they abut on the inner cell-wall, next the cavity of the sporangium (fig. 31, A and B). In a tangential section of the whole strobilus, which gives a transverse section of the sporangium, the cells of the wall are cut across, so that we see the buttresses on either side of each vertical septum (fig. 31, B). In transverse or radial sections of the strobilus, however, which give longitudinal sections of the sporangia, the cells of the wall are cut lengthwise. In this case the narrow edges of the buttresses are seen, so that the vertical septa appear to be much more numerous than they really are (fig. 31, C). The actual cell-walls are seldom seen well in this view, no doubt because they are usually cut obliquely. The mode of thickening of the cell-membranes of the sporangial wall bears a considerable resemblance to that of the "fibrous layer" of some anthers, and may very probably have discharged the same function, that of effecting dehiscence.

In certain cases a layer of thin-walled tissue, two or three cells in thickness, is found lining the whole or part of the sporangial wall (Plate 82, fig. 35). One is tempted at first to regard this layer as a persistent *tapetum*, but the inconstancy of its occurrence, even in the most perfectly preserved specimens, and its very variable thickness when present, are scarcely consistent with such a view. In other instances the entire

* See also WILLIAMSON, "Organization," Part XI., Plate 54, fig. 23 (C.N. 1017).

sporangium appears to be filled with parenchymatous tissue.* These apparently parenchymatous sporangia are sometimes associated in the same strobilus with others which show the lining tissue only.†

It is a question whether such sporangia are ever really filled with tissue, or whether the sections may not in these cases be tangential to the sporangium, so as to pass through the lining layer, without reaching the spores within. This is a possible view, but we do not think that all these instances can be thus explained. The sporangia with parenchymatous contents cannot represent a normal early stage of development, for they occur side by side with others in which the spores are fully formed, and in which there is often no trace even of the lining tissue. On the whole we are disposed to regard all the structures in question as representing more or less completely abortive sporangia in which either the whole, or the outer portion only, of the sporogenous tissue has remained sterile. This view is supported by the relatively small size of those sporangia which appear to be completely filled with parenchymatous tissue.

D. The Spores.

It has long been known that the spores of *Calamostachys* are often found associated together in tetrads, each tetrad being enclosed within a common membrane, which is doubtless the wall of the mother-cell. Cases of this kind have been figured in previous memoirs,‡ and have also been observed and figured by M. RENAULT in allied fructifications.§ The latter author lays great stress on the arrangement of these cells in tetrads, regarding this fact as an argument for the bodies in question being of the nature of pollen-grains, rather than spores.||

In *Calamostachys Binneyana*, at any rate, there is no ground for such a view, for the spores certainly did not remain associated in tetrads when mature. Isolated spores are just as common as tetrads, and sometimes occur together with them in the same sporangium (see Plate 81, fig. 33), while in other cases the whole sporangium is occupied by isolated spores.¶ The separation of the sister-spores from one another must have taken place relatively late, but it certainly happened before maturity.

We have paid special attention to the spore-tetrads, which are shown on various scales, in Plate 81, fig. 33, and Plate 82, fig. 34. In some cases the group of four spores is perfectly normal, all four being of approximately equal size (fig. 34, A). Very often, however, the spores of the same tetrad are of extremely unequal dimen-

* An example of this has been previously figured; see WILLIAMSON, "Organization," Part X., Plate 16, fig. 18.

† As is the case, for example, in C.N. 1008, and 1898 A.

‡ WILLIAMSON, "Organization," Part V., Plate 7, fig. 43, Part X., Plate 15, fig. 17.

§ *E.g.* in his *Bruckmannia Grand'Euryi*, 'Ann. Sci. Nat., Bot.,' Sér. 6, vol. 3, Plate 3, Fig. 7.

|| 'Comptes Rendus,' vol. 102, March 15, 1886.

¶ See WILLIAMSON, "Organization," Part V., Plate 6, fig. 7 (C.N. 989).

sions, the diameter of the smallest sister-cell being often scarcely a quarter that of the largest. Sometimes three out of the four remain quite small, and occasionally an entire tetrad seems to have been abortive (see the figures cited; in fig. 34, B and C, one spore in each tetrad is of relatively minute size).

Such very minute spores are also frequently found, among the normal ones, in sporangia in which the spores are already isolated from one another. If these latter cases stood alone, we might have doubted whether the small spores were not foreign bodies; their presence, however, as members of the tetrads, within the mother-cell-wall, proves conclusively that they are really sister-cells which have remained behind the others in their development. The phenomenon is extremely frequent, as is sufficiently indicated by the figures.

We do not think there is any reason to doubt that four spores were regularly formed within each mother-cell, as is constantly the case in all recent vascular Cryptogams. It seems, however, to have been the exception for all four to be equally developed.

This frequent abortion of many of the spores in a sporangium, so frequent that we cannot but regard it as a normal process, seems to us to be a fact of extreme interest.

We cannot doubt that *Calamostachys Binneyana* was a homosporous form. The large number of specimens available for investigation, many of them including all parts of the strobilus, establishes the strongest presumption that macrospores must have been found, if they existed.

We know, however, that the closely similar species, *C. Casheana*, was heterosporous, its microspores not being very different in size from the normal spores of *C. Binneyana*. When we come to describe the heterosporous species, we shall find strong reason to believe that in its macrosporangia a constant abortion of some of the spores went on.

We would suggest the hypothesis that the abortion of certain of the spores, and the consequent increased nutrition of their surviving fellows, may have been the physiological condition which ultimately rendered possible the development of specialized macrospores.

We know that among existing heterosporous vascular Cryptogams the abortion, either of the majority of the mother-cells (Ligulatæ), or, in addition, that of the sister-cells of the macrospore (Rhizocarpeæ), is a constant accompaniment of the favoured development of the surviving spore or spores.

We know also that in *Equisetum*, which is homosporous, but in which the prothalli are regularly diœcious, it depends upon the nutrition whether a spore develops into a male or female prothallus. The better fed prothalli become female, the worse fed, male.*

In *Calamostachys* we have the intermediate conditions. In *C. Binneyana* we find the beginning of spore-abortion, involving improved nutrition of the surviving spores.

* BUCHTIEN, "Entwickelung des Prothalliums von *Equisetum*," 'Bibliotheca Botanica,' 1887.

In *C. Casheana*, the same process, carried further in certain sporangia, has led to the formation of specially favoured macrospores, to which, as we may presume, the production of a female prothallus was entrusted. Even in *C. Casheana*, however, the heterospory is not so extreme as in some other Cryptogams, for numerous macrospores are still developed in each sporangium, and their diameter is only about three times that of the microspores.

We suggest then, that in *Calamostachys* we have a genus in which the first rise of the phenomenon of heterospory can be traced. That the same phenomenon arose independently in various groups of vascular Cryptogams, has long been recognized.

We have found no evidence in *C. Binneyana* for the existence of a cellular body within the spore, such as M. RENAULT believes to be present in the spores of this and other species. One of us (D. H. SCOTT) has had the advantage, through the kindness of M. RENAULT, of seeing some of the preparations in question, but was not convinced that the structure within the spore was really cellular.

Compared, for example, with the cellular mass in the pollen-grain of *Cordaites*, as shown in M. RENAULT'S classical preparations, the appearances in the *Calamostachys* spores appeared very doubtful. In our own specimens, the endosporium has usually contracted away from the exosporium. When the endosporium and its contents are much shrivelled, an appearance resembling a cellular structure is sometimes produced, but such appearances are quite inconstant, and are, we believe, illusory.

In the mature spores of *Calamostachys Binneyana* we often observe three radiating cracks at one pole, such as are so frequently seen in the spore-membranes of recent Cryptogams. Between these cracks three well-defined brown masses can usually be detected. In sectional views of the spore we find that these bodies are attached to the inner surface of the spore-membrane (see Plate 81, fig. 33*a*; Plate 82, fig. 34, D). Other specimens proved that the attachment is to the exosporium. We regard these masses as local thickenings of the cell-wall, not by any means as distinct cells.

Before discussing further the affinities of *Calamostachys Binneyana*, it will be necessary to take into consideration the structure of the other forms which we have examined.

CALAMOSTACHYS CASHEANA. WILL.

The heterosporous form of *Calamostachys* was originally described in 1880* from a specimen found at Halifax. In this specimen three whorls of sporangia are shown in the obliquely tangential section. The uppermost whorl shows microsporangia only; in the lowest, only macrosporangia are found, while the intermediate whorl contains both kinds intermixed.

The general habit of the specimen is very similar to that of *C. Binneyana*, with

* WILLIAMSON, "Organization," Part II., p. 298; Plate 54, fig. 24 (C.N. 1024 and 1025). M. RENAULT has also established the existence of heterospory in *Annularia longifolia*, BRONGN. 'Ann. Sci. Nat., Bot.,' sér. 5, vol. 18, 1873. (Also in 'Cours de Botanique Fossile,' vol. 2, 1882, p. 126.)

which it was at first regarded as identical. Subsequently the species *C. Casheana* was established for the heterosporous form.*

Apart from the heterospory, there are some slight differences between the species. While in *C. Binneyana* both bracts and sporangiophores stand out exactly at a right angle with the axis, in *C. Casheana* they seem to have been placed rather obliquely, sloping slightly upwards. Further, in a tangential section of *C. Casheana,* passing through the sporangia, the bracts are beginning to separate from one another; whereas in similar sections of *C. Binneyana*, they form a perfectly coherent disc. It appears then, that the coherent portion of the bracts did not extend so far in the heterosporous as in homosporous species (see Plate 74, photograph 15). These differences, however, are very slight, and it is certainly a most striking fact that species so nearly alike in general characters should exhibit so important a physiological distinction as that between homospory and heterospory.

A second specimen of *C. Casheana*, obtained from the Strinesdale Pit, Saddleworth, has more recently been discovered. Two sections have been cut of the strobilus, the one tangential (Plate 74, photograph 15), the other transverse (photograph 16). The former shows parts of three verticils of sporangiophores; the highest and lowest verticils show macrosporangia only; the intermediate whorl also contains a single microsporangium, which is borne on the same sporangiophore with three macrosporangia (photograph 15, also Plate 82, fig. 38). The relative size of the microspores and macrospores agrees exactly with that in the former specimen, *i.e.*, the diameter of the macrospores is, on the average, just three times that of the microspores. The absolute dimensions of both are perhaps a trifle smaller than in the original specimen, but the difference is insignificant.

The transverse section of this strobilus (C.N. 1588, Plate 74, photograph 16; Plate 82, fig. 36) is very interesting. The section passes through macrosporangia only; the pedicels of the sporangiophores are cut obliquely, which agrees with their ascending direction, as shown in the other specimen.†

The structure of the axis is extremely well shown, and agrees exactly with that of *C. Binneyana.* The axial cylinder, or stele, is of the obtusely triquetrous form, and has a somewhat sclerotic pith. The arrangement of the vascular bundles agrees with that of the homosporous species. Traces of the protoxylem-groups are found in the usual position, namely within irregular gaps on the inner side of the vascular bundles, of which there seem to have been six altogether.

The most interesting point, however, is that the axis has a well-marked zone of secondary wood (see fig. 36); the radial arrangement of its elements is such as to leave no doubt as to their origin. We thus find in this specimen the direct proof that secondary growth in thickness co-existed with heterospory; in other words the

* WILLIAMSON, in 'Report of the British Association for 1886.'

† C.N. 1024. See WILLIAMSON, *loc. cit.*, Part XI., Plate 54, fig. 24.

specimen is, by itself, sufficient to prove the occurrence of secondary formation of wood in an undoubted Cryptogam.

It is probable that no botanists any longer dispute the conclusion that secondary growth by means of cambium may take place in Cryptogams as well as in flowering plants, or that in the Carboniferous epoch, most families of vascular Cryptogams exhibited this phenomenon. The "*petitio principii* of BRONGNIART's school,"* which for so long a time was accepted by many leaders of botanical opinion, is no longer maintained. Evidence so direct and convincing as that afforded by this specimen of the hetorosporous *Calamostachys* is, however, sufficiently rare to be of quite special interest.

Some remains of the thin-walled tissue which surrounded the wood are preserved, but, as is usually the case, very imperfectly. The outer cortex, on the other hand, is perfect, and has the same structure as in *C. Binneyana*, the cells becoming smaller and more sclerotic towards the periphery.

The details of structure of the bracts, the sporangiophores, and the sporangium-wall agree so closely with the corresponding features in the homosporous species, that no special description is called for.

The Spores.

We have already (p. 911) referred to the small, presumably abortive spores, found in the macrosporangia, among the macrospores. Their dimensions are very variable, but they are always much smaller even than the microspores of the same strobilus. (See figs. 37 and 39, which are from different specimens.) They are very similar to the abortive spores described above, in the case of *Calamostachys Binneyana*. As we never found the tetrad stage in *C. Casheana*, there was no possibility of tracing the origin of these minute spores. They occur, without exception, in every macrosporangium of both specimens, and are often found in large numbers. (See fig. 37, B and C; fig. 39.) We have never found them in the microsporangia. For these reasons we think it out of the question that the minute spores can be foreign bodies. We regard them as being, in all probability, undeveloped sister-cells of the macrospores, the latter having attained their large dimensions at the expense of their ill-nourished companions.

We desire especially to call attention to the fact that we find no signs of spore-abortion in the microsporangia. Here all the spores appear to develop equally, and a uniform small size is attained (about ·075 millim. in diameter). In the homosporous species, *C. Binneyana*, where some of the spores are abortive, the survivors attain somewhat greater dimensions, about ·09 millim. in diameter.

As regards the structure of the spores, we have little to add to the previous description above cited. Apart from the difference in size, there is a close similarity

* SOLMS, 'Fossil Botany,' p. 330 and 341.

between macrospores and microspores. In both we find a thick exosporium, within which, and somewhat separated from it, is a much more delicate membrane, which we will term the endosporium. In the case of the macrospores, the exosporium is often somewhat flattened at the surfaces of contact of the rather closely packed spores. Within the endosporium, in both microspores and macrospores, is usually a relatively small, dark-coloured mass, probably representing the carbonized remains of the cell-contents.

The more recently discovered specimen is, in one respect, better preserved than the one originally described. In the latter, the endosporium is almost always somewhat shrivelled, in the case of both micro- and macrospores. In the former, the endosporium has usually retained a perfectly spherical form; the exosporium, however, has often, to some extent, split away from the inner layer.

It may be mentioned that in one or two cases the exosporium appeared to be double, so that, very probably, an episporial membrane was present, but cannot usually be distinguished.

In the case of the small abortive spores, associated with the macrospores, it was not possible to distinguish the separate layers of the cell-wall.

Calamostachys, *sp.?*

A specimen of *Calamostachys* from the Oldham Coal-Measures, shows a somewhat different habit from *C. Binneyana* (see Plate 74, photographs 17 and 18). Both bracts and sporangiosphores have the same obliquely upward direction which we observed in *C. Casheana.* Five whorls of sporangiophores, with their sporangia, are present in the specimen. The latter are filled with small spores (not associated in tetrads), which agree precisely in dimensions with the microspores of *C. Casheana.* It is possible that the specimen may belong to that species, the macrosporangia not being preserved. No certain conclusion, however, can be drawn, except that the specimen is at any rate not identical with *C. Binneyana.*

Affinities of *Calamostachys.*

The description given of the structure of the strobilus in the homosporous and the heterosporous species, leaves no doubt that both must have been the fructifications of Calamarieæ. In view of the close agreement in structure which we have been able to demonstrate, the suggestion of M. Renault that while the heterosporous forms are obviously cryptogamic, the others may represent the male flowers of seed-bearing plants, appears to us to be quite untenable.

The whorled appendages, the constant presence of a medulla, and of primary medullary rays, and the collateral bundles with centrifugal xylem, form a combination of characters peculiar to the Calamarieæ among the known Cryptogams of the

Carboniferous epoch. The arrangement and structure of the peltate sporangiophores, so closely resembling those of *Equisetum,* are typical of *Calamarieæ,* and indeed constitute the most essential characters on which that family has been founded.

The question remains, however, to which, if any, of the known Calamarian stems, did the *Calamostachys* fructifications belong? At present the question must remain open, for the only way of answering it with certainty, would be to find stem and strobilus in connection, and this has not yet been done in the case of the species in question.

So far as the anatomical evidence is concerned, there is no reason why a strobilus of the *Calamostachys* type should not have been borne on the stem of a Calamite, such as we have described in the first part of this paper. The differences in structure are no greater than we should be prepared to find between the axis of a fructification and a vegetative stem, and no greater than we actually do find between branches of different order in one and the same species of *Equisetum.* In some points, indeed, such as the presence of an intercellular space at the protoxylem of each bundle, and the structure of the nodal wood, the agreement is even surprisingly close.

We have, however, to take account of the fact that a fructification of a different type has been proved, in previous memoirs, to have been that of a *Calamites.* The first specimen of this fructification was described in 1869.* Long subsequently other and more complete specimens were discovered, and a full account of the whole structure was laid before the Royal Society in 1887.† We have re-examined the specimens for the purposes of the present paper, but, except in one point, have nothing to add to the previous descriptions.

A summary, however, of the facts relating to this fructification must be given here, for the sake of comparison with the structure of *Calamostachys.*

The strobilus of the "Calamitean" fructification was pedunculate, and consisted of an axis bearing numerous whorls of bracts, which were coherent for some distance from their insertion, the coherent part forming the "disk" of previous descriptions. The bracts after leaving the axis at a right angle, or with a slightly downward curvature, turned sharply upwards, their superior portions becoming approximately parallel to the axis.

The sporangiophores were borne at the base of the coherent bracts, on their upper surface, and were thus very nearly axillary. They numbered sixteen, eighteen, or twenty in a whorl; their direction was obliquely upward. The number of the bracts seems to have been double that of the sporangiophores.

Each sporangiophore bore four sporangia, though it is not quite certain that this number was absolutely constant. They surround the pedicel of the sporangiophore, as

* WILLIAMSON, 'Mem. Lit. and Phil. Soc. of Manchester,' Series 3, vol. 4.

† WILLIAMSON, "True Fructification of *Calamites*" ("Organization," Part XIV.); 'Phil. Trans.,' vol. 179, B.

in *Calamostachys*. As no peltate expansion is preserved in the specimens, there is no evidence as to the mode of attachment of the sporangia.

In tangential sections the sporangia have an elongate, oblong form, thus differing from those of *Calamostachys*, which appear square in the corresponding view. This difference, however, seems to depend only on the oblique position of the sporangia in the "Calamitean" fructification.

The sporangial wall resembled that of *Calamostachys* in structure. The spores are all of approximately equal size, and average ·075 millim. in diameter. As sections were cut from all parts of several strobili, including their bases, it is not probable that macrosporangia, if they had existed, could have been missed.

The anatomy of the peduncle is exactly that of a young stem of *Calamites*, as above described. The pith is fistular, only the peripheral zone being persistent. The wedge-shaped bundles, sixteen to twenty in number, form a ring. Each bundle has a canal at its inner margin. We have been able to prove that here, as in the vegetative stems of *Calamites*, the canal contains the remnants of the protoxylem of the bundle. In longitudinal sections the spiral thickenings of the primitive tracheides in the canal can be easily seen.*

Secondary wood, distinguished by the radial seriation of its elements, was formed in the peduncle just as in the vegetative stem. In fact the peduncle agrees in every respect with the typical vegetative axis of a young specimen of *Calamites*.

The axis of the strobilus has essentially the same structure as that of the peduncle, of which it is the prolongation. The number of the bundles, which is equal to that of the sporangiophores, remains constant. Their structure is unaltered, except that, as we ascend the axis, we leave the secondary wood behind. At the nodes the arrangement of the tracheides is identical with that in *Calamites*. The bundles however show a slight difference in their arrangement. In the peduncle they are equidistant from one another; in the axis of the strobilus they become approximated in pairs. The cortex contains a ring of large cavities, half as numerous as the bundles, and alternating in position with the bundle-pairs. These cavities, which recall the "vallecular canals" of *Equisetum*, are best seen at the nodes, where the cortical tissues are best preserved.

Now there can be no doubt that this remarkable fructification, specimens of which are unfortunately extremely rare, is that of a *Calamites*. If the peduncle were found alone it could not be distinguished from the stem, of corresponding age, of a typical Arthropitoid Calamite.

We wish to call attention to the very close resemblance between this strobilus of *Calamites*, and that described by M. RENAULT under the name of *Volkmannia gracilis*, but placed by Count SOLMS-LAUBACH in WEISS's genus *Palæostachya*.† In the

* C. N. 1569 and 1573.

† RENAULT, 'Ann. Sci. Nat., Bot.,' Sér. 6, vol. 3, Plate 2; also 'Cours de Bot. Fossile,' vol. 2; SOLMS, 'Fossil Botany,' p. 332.

latter specimen the relative position of the bracts and sporangiophores is all but identical with that in the English fossil. The chief differences are that the bracts in *Palæostachya gracilis* are less extensively coherent, and that the insertion of the sporangiophores is more exactly axillary, and less adherent to the bracts themselves. In both plants the number of the bracts is double that of the sporangiophores.

The anatomy of the stem in *Palæostachya gracilis,* as shown in M. RENAULT's figures, has quite a Calamitean character. The medulla is fistular, and the vascular bundles are accompanied by their usual canals. The number of the bundles here also, is equal to that of the sporangiophores.

In M. RENAULT's plant the peltate scales are perfectly preserved; their structure and the mode of attachment of the sporangia are manifestly the same as in *Calamostachys.*

The character of the genus *Palæostachya*, as defined by WEISS, is as follows:

"Sporangiophores arising from the axil of the bract, or its immediate neighbourhood, ascending obliquely."*

As this definition applies both to the Calamitean fructification of WILLIAMSON, and to the *Volkmannia gracilis* of RENAULT, we may speak of this type as the *Palæostachya* form of fructification. As however the English specimens are so obviously strobili of *Calamites*, we do not propose to give them a distinct generic name, but to distinguish them as *Calamites pedunculatus*, which is thus the equivalent of the "true fructification of *Calamites*," described in previous memoirs.

We have now to discuss this question: Are the differences between the *Calamostachys* and the *Palæostachya* types of strobilus so great that they cannot have belonged to closely allied plants?

The essential differences are two: (1) in the position of the sporangiophores, which are approximately axillary in the *Palæostachya* type, but are inserted midway between the whorls of bracts in *Calamostachys;* (2) in the anatomy of the axis, which is completely Calamitean in the *Palæostachya* strobilus, while *Calamostachys* differs in the small number of vascular bundles, and in its relatively small persistent pith.

A form described by M. RENAULT under the name of *Bruckmannia Grand'Euryi* (the *Calamostachys Grand'Euryi* of WEISS's nomenclature) seems to bridge over the gap in a very satisfactory manner.† In this species the arrangement of the sporangiophores is exactly that of a typical *Calamostachys;* they form independent whorls, inserted midway between the verticils of bracts. Their structure, also, is identical with that of the sporangiophores of *C. Binneyana.* The anatomy of the axis, however, is that of a Calamite. The medulla is large and fistular; the numerous bundles surrounding it have well-defined canals. It appears, then, that in this species the external morphology of *Calamostachys* co-existed with an anatomical structure identical with that of *Calamites* or *Palæostachya.*

* 'Steinkohlen-Calamarien,' vol. 2, 1884, p. 161.

† RENAULT, 'Ann. Sci. Nat., Bot.,' Sér. 6, vol. 3. Plates 3 and 4.

In view then of the fact that a renewed examination of *Calamostachys Binneyana* has tended to show that its anatomy is much more similar to that of *Calamites* than was formerly supposed, while another species of the genus has an exactly Calamitean structure, we think that the relation of our British species of *Calamostachys* to *Calamites* may well have been a close one. It is even possible that some of the stems which have been described under the general name of *Calamites*, may have been those on which *Calamostachys* fructifications were borne.* Beyond this we cannot go, until evidence of continuity has been produced. We know for certain that the *Palæostachya* type of strobilus was that of a Calamite, as is proved by the case of *Calamites pedunculatus;* it is possible that fructifications of the *Calamostachys* type may have belonged to other Calamitean stems.

The solution of the problem must await further evidence.

III. SPHENOPHYLLUM.

The genus *Sphenophyllum*, BRONGNIART, is characterized externally by its comparatively slender, articulated stems, bearing verticillate leaves, the number of which in each whorl is always some multiple of 3, as 6, 9, 12, 18, or even more. The leaves of successive verticils are superposed, not alternate. In the species on which the genus was founded (such as *Sphenophyllum Schlotheimii*, BRONGN., and *S. emarginatum*, BRONGN.), the sessile leaves are cuneate, widening rapidly from a narrow base, and having an entire or toothed anterior margin. From the form of such leaves as these the genus derived its name. In other species, however, the leaf is repeatedly divided in a dichotomous manner, into narrow segments, as in *S. trichomatosum*, STUR. In others, again, as in *S. plurifoliatum*, WILL., one of the species which we are about to describe, the leaves are linear.

The forms with deeply divided, or with linear leaves, cannot always be distinguished, by their external characters alone, from *Asterophyllites*, to which genus the species about to be described were originally referred.† Happily the anatomy of several undoubted species of *Sphenophyllum* is now well known,‡ and agrees in all essentials with that of our own specimens, which have already been transferred to that genus.§

It is said that the finely divided foliage may occur on the lower portions of the same stems which bear cuneate leaves above.|| This has been compared with the

* Mr. T. HICK, in his paper above cited (see p. 905) arrives at substantially the same conclusion; *loc. cit.*, p. 291.

† WILLIAMSON, "Organization," Parts V. and IX.

‡ Chiefly through the researches of M. RENAULT, 'Ann. Sci. Nat., Bot.,' Sér. 5, vol. 18, 1873, and Sér. 6, vol. 4, 1877; also 'Cours de Bot. Fossile,' vols. 2 and 4.

§ WILLIAMSON, 'General, Morphological, and Histological Index,' Part 2, p. 3, 1893.

|| COEMANS et KICKX, "Monographie des Sphénophyllum d'Europe," 'Bull. de l'Acad. Roy. de Belgique,' Sér. 2, vol. 18, 1864.

arrangement of the leaves in the heterophyllous species of *Ranunculus*, of the sub-genus *Batrachium*. Several authors have inferred that *Sphenophyllum* was of aquatic or at least semi-aquatic habit. The anatomy, however, as other authors have already pointed out,* lends no support to such a view, for in all cases the xylem is extremely well developed, whereas its reduction is one the most constant characteristics of aquatic plants.

The species which we are about to consider are three in number :

(1.) *Sphenophyllum plurifoliatum*, identical with the *Asterophyllites sphenophylloides* of WILLIAMSON (Parts 5 and 9). This includes the Oldham specimens.

(2.) *Sphenophyllum insigne*, the *Asterophyllites insignis* of the memoirs above cited. To this the Burntisland specimens belong. In these two we know only the vegetative organs.

(3.) *Sphenophyllum Dawsoni*. This is the *Bowmanites Dawsoni* of previous memoirs,† and the *Volkmannia Dawsoni* of BINNEY. The specimens of this form are, with one exception, limited to the fructifications.

We will begin with the Oldham species, *S. plurifoliatum*, which, in its internal structure, agrees most nearly with the species described by other authors.

1. SPHENOPHYLLUM PLURIFOLIATUM, NOBIS.

Although this form has not been identified with any of the species known as impressions, yet the fragments showing structure are sufficient to give also a general idea of the external morphology.

The stems are conspicuously jointed with somewhat tumid nodes.‡ The internodes are of considerable length, amounting to about 1 centim. in one of our specimens,§ which shows two nodes, but no doubt much more in others.

In no case is a complete whorl of leaves preserved; judging, however, from specimens such as C.N. 874,‖ in which the bases of 6 leaves are shown, the total number in the verticil could not have been less than 18, and may even have reached 24. The leaves are sometimes preserved for a considerable part of their length, exceeding that of the internode. They remain linear in form throughout, so far as can be seen, and there is no distinct evidence for their dichotomizing, though they may have done so at some considerable distance from the base.¶

The cortex of the young stems, as shown in transverse sections, has a very charac-

* See SOLMS, 'Fossil Botany,' p. 344.

† WILLIAMSON, "Organization," Parts XVII. and XVIII.

‡ See WILLIAMSON, "Organization," Part V., Plate 3, fig. 15, and Plate 1, fig. 5.

§ C.N. 904.

‖ Figured in WILLIAMSON, *loc. cit.*, Part V., Plate 3, fig. 16.

¶ M. ZEILLER has shown that truly linear leaves also occur in *S. cuneifolium*, STERNB. See his paper in 'Mém. de la Soc. Géol. de France; Paléontologie,' Mém. 11, p. 13, 1893.

teristic outline.* There are three sharp depressions, or furrows, which bear a definite relation to the internal structure, each depression lying midway between two of the prominent angles of the triquetrous strand of primary wood. The cortical surfaces between the furrows are nearly flat. This is the form in the internode; close to the nodes, however, a secondary elevation is found in the middle of each furrow.†

The characteristic outline of the cortex agrees with that in several other species of *Sphenophyllum*.‡ It is only to be observed in the younger stems, for, as we shall see, the whole primary cortex soon becomes replaced by periderm, and cast off.

We will now describe the anatomical structure. Many points can be passed over rapidly, as they have already been sufficiently dealt with in the previous memoirs above cited.

Primary Structure.

The stem is traversed by a vascular cylinder or stele, the primary structure of which is simple, though, for a stem, highly peculiar.

The wood, as seen in transverse section, is triangular; the sides of the triangle are somewhat concave, the angles are slightly truncated. The xylem is a solid mass of tracheides; there is no trace either of a medulla or of xylem-parenchyma. The tracheides near the middle of the stele are pitted, and of large size; as we approach the three prominent angles we find that the size of the tracheides rapidly diminishes, and their walls have here scalariform thickening. At the actual angles we find reticulated and spiral elements of very small diameter (see Plate 83, figs. 40 and 41). There can be no doubt that the tracheides at the angles are the primitive elements, or protoxylem, and that the primary wood constitutes a centripetal triarch strand—a structure which is very unusual in stems, though so familiar in the case of roots.

The angles of the triquetrous xylem are often blunt, though this is not always the case. We could not convince ourselves that more than a single group of protoxylem is present at each angle, though, in other species, there are undoubtedly two such groups, and the stele is then hexarch (see Plate 76, photograph 24, from the Autun *Sphenophyllum;* also many figures in M. RENAULT's works above cited).

The wood is surrounded by a thin-walled tissue of considerable width, but in the youngest specimens, such as we are now describing, this zone is seldom well preserved. The cells near the wood are smaller than those more towards the exterior. We can hardly be wrong in regarding the tissue immediately surrounding the wood, as phloëm; the outer thin-walled region is, perhaps, best interpreted as a pericycle, in which case we should take the commencement of the more peripheral thick-walled zone as the inner limit of the cortex. It must, however, be remembered that, in the

* See WILLIAMSON, *loc. cit.*, Part V., Plate 1, fig. 1, &c.

† WILLIAMSON, *loc. cit.*, Part V., Plate 1, fig. 4.

‡ See RENAULT, *loc. cit.*

absence of developmental data, such delimitation of the tissues is necessarily arbitrary.

The thin-walled zone is very sharply marked off from the rather sclerotic cortex. The latter consists of somewhat elongated cells, which become narrower and more sclerenchymatous as the exterior is approached. The structure of the epidermis is not clear in any of our specimens.*

The vascular system is strictly *cauline;* it passes through the nodes without any appreciable change of structure. A single bundle entered each leaf; from the analogy of other species of *Sphenophyllum,* it may be presumed that the foliar bundles were given off from the angles of the central strand. The number of foliar bundles given off at each node cannot have been less than eighteen.† It is possible that these may have arisen from the subdivision, within the cortex, of a smaller number, but as regards this species, such a conclusion is merely conjectural.

For the mode of *branching* of the stem, we have only the evidence of one preparation.‡ In this case a single branch evidently arose at the node; its vascular cylinder was to all appearance given off from one of the angles of the stele of the main stem.

Secondary Changes.

In *S. plurifoliatum,* as in other species of the genus, a large amount of secondary tissue, both wood and bast, was formed in the stem as growth proceeded. We have specimens with the secondary wood of every thickness, from a single layer of elements up to thirty-seven such layers. Some of the stages have already been figured.§ Others are illustrated in the photographs and figures accompanying the present paper. There is no break in the series, and, except for the changes involved in the secondary growth itself, the structure is the same in all. Hence there is no doubt that we are dealing with successive stages in the development of one and the same plant. The great extent of the secondary cortical tissues is a characteristic feature of the genus.

We will begin our description with the secondary wood.

The radial seriation of the elements is in most cases remarkably regular (see the photographs on Plate 75; also Plate 83, figs. 40–43). In one large specimen, for example, the rows are quite continuous throughout the secondary wood, which here attains a thickness of twenty-four elements (photograph 21). The same is the case in the specimen, a portion of which is shown, in transverse section, in photograph 22. Here the maximum thickness of the wood is thirty-seven elements.

* For the details of primary structure, just described, reference must be made to the Memoirs of WILLIAMSON above cited.

† See WILLIAMSON, *loc. cit.*, Part IX., Plate 21, fig. 28 (C.N. 908).

‡ C.N. 908, see figure just cited.

§ See WILLIAMSON, *loc. cit.*, especially Part V.

In some other cases the regular seriation is disturbed by the presence of a more or less complete zone of smaller xylem-elements, at first suggesting the idea of an annual ring. No such explanation however is admissible, for these small-celled regions are of very inconstant occurrence, and, when present, they by no means always extend round the entire circumference. Evidently the young wood-cells underwent some additional subdivisions in these zones. Beyond them, the regular radial series of large elements are resumed.

Occasionally these slight irregularities co-existed with a very unequal growth of the opposite sides of the stem. Extreme cases of this kind have been previously figured.* These excessive irregularities are quite exceptional, and were no doubt due to some accidental interference with the normal growth.

The structure of the secondary wood is highly characteristic. The large elements, which in transverse section appear nearly square, often with truncated corners, are tracheæ. Their radial walls are marked by numerous small pits (see Plate 83, figs. 40, 42, 44, and 44A) of somewhat oval outline. When the wall is seen in section it appears that these pits were bordered.

Pits are also sometimes found on the tangential walls, but less constantly. As regards the structure of their walls, the secondary tracheæ are quite similar to those of the middle portion of the primary xylem, except that the latter are pitted equally on all surfaces (see Plate 83, figs. 40 and 41).

A more important difference is the fact that the primary elements have pointed ends, and are no doubt to be regarded as tracheides, while the secondary tracheæ appear to form continuous tubes. It is possible that the latter were really vessels, but the evidence is insufficient to prove this. We shall see that the supposed remains of transverse walls are really of quite a different nature.

Between the corners of the tracheæ we find parenchymatous cells, occupying the space left free by their truncated angles. (See Plate 75, photographs 20 and 22; also Plate 83, figs. 43 and 44A.) Occasionally one such cell appears in the transverse section, in each space; more often there is a little group of them, sometimes six or more in number.

Every here and there the transverse section shows a radially placed cell, or a strand of two or three such cells, side by side, passing between the tracheæ, and uniting the parenchymatous groups with one another.

In a radial section we see that the thin-walled parenchymatous cells at the corners of the tracheæ, form longitudinal strands of considerable length, which are connected at intervals by the radially elongated cells. (See Plate 83, figs. 44 and 44A.)

In a tangential section of the wood, only the lenticular cross-sections of the horizontal parenchymatous cells are seen, for none of them lie in a tangential plane.†

It was these radial parenchymatous cells which M. RENAULT at one time regarded

* WILLIAMSON, *loc. cit.*, Part V., Plate 2, figs. 11 and 12.

† See WILLIAMSON, *loc. cit.*, Part V., Plate 2, fig. 13.

as the remains of transverse walls in the tracheæ,* a view which he has elsewhere abandoned in favour of the true explanation.†

The arrangement of the cells, two or three of which are often placed immediately above one another (see fig. 44) is quite inconsistent with the former view, which is also negatived by the fact that no such transverse markings are seen in a tangential section.

It is important to notice that the radial cells in question do not, as a rule, form *continuous* radial series, and thus differ from the true medullary rays, such as are present in *Sphenophyllum insigne.* (Compare Plate 83, fig. 44, with Plate 84, fig. 49.) It must, however, be pointed out that the absence of continuous medullary rays is not constant even in *S. plurifoliatum.* In the outer layers of the secondary wood, continuous radial tracts of parenchyma, sometimes several cells in breadth, make their appearance. (See Plate 75, photograph 22.)

The description given so far applies more especially to that part of the secondary wood which is formed *between* the angles of the primary xylem; we may term this part of the wood *interfascicular*, using this term for the tissue formed between the protoxylem-groups, in contradistinction to that which is formed opposite them; for the latter the term *fascicular* wood will be used.

The fascicular wood is sharply distinguished from the interfascicular, as seen in transverse sections. (See Plate 75, photographs 19, 20, and 21; Plate 83, fig. 43.) This is due in the first place to the much smaller dimensions of the fascicular tracheæ. The secondary wood is necessarily thinnest opposite the prominent angles of the primary xylem, for the general outline of the wood becomes circular as soon as secondary growth is established. The number, both of tangential and radial series is, however, usually greater in the fascicular region, so the reduced size of the elements here is easily explained. There is a general continuity of the concentric series of xylem-elements all round the stem; the fascicular cells have simply undergone some additional subdivisions. The structure of the tracheæ is the same in both regions. The most important distinction consists in the presence of continuous medullary rays, from the first in the fascicular wood, while in the interfascicular region, they only appear, if at all, in the outer layers. The boundary between fascicular and interfascicular wood is fairly sharp in the inner secondary zones; the distinction, however tends to disappear in the outer part of the wood of very old stems (see photograph 21).

That the whole zone of wood, outside the triquetrous strand, is really secondary, has been sufficiently shown by M. VAN TIEGHEM.‡ In *Sphenophyllum plurifoliatum*, we are able to give the final proof, for in several of our specimens the cambium itself,

* 'Cours de Botanique Fossile,' vol. 2, p. 99, 1882.

† 'Ann. des. Sci. Nat., Bot.,' Série 6, vol. 4, p. 297, Plate 8, figs. 2 and 4, 1877 (*sic*). 'Cours de Botanique Fossile,' vol. 4, p. 8, Plate C, fig. 4, 1885.

‡ "Sur quelques points de l'Anatomie des Cryptogames Vasculaires." 'Bull. de la Soc. Bot. de France,' vol. 30 (1883), p. 169.

by which the secondary tissues were formed, is well preserved. It is especially evident in the section from which fig. 42 on Plate 83 was drawn, in which the correspondence of the thin-walled tabular cambial-cells, with the radial series of secondary tracheæ, is perfectly clear. Other specimens in which the cambium is preserved, are illustrated in the photographs 19 and 20 on Plate 76.

A relatively enormous amount of secondary cortical tissue was developed on the outer side of the cambium (Plate 75; Plate 83, figs. 40 and 43). It is often difficult to distinguish, in transverse sections, between the true phloëm, formed directly from the cambium, and the internal periderms, which arose in abundance from deeply-seated layers of phellogen. The transverse section, shown in photograph 19 and in fig. 43, is especially instructive. Here the actual cambium is only partially preserved; immediately outside it the wide secondary cortex* begins. At the place shown in fig. 43, its maximum thickness was about 16 cells.† The radial series are continuous throughout, and a general continuity with those of the wood can also be traced. The inner zones of the secondary cortex consist of thin-walled cells; each cell is occupied by a carbonaceous mass (omitted in the figure for the sake of clearness, but recognizable in the photograph). This carbonaceous matter may perhaps indicate the original presence of abundant cell-contents. The outer cortical layers are formed of cells with much thicker walls, and without any considerable carbonaceous contents. Between the two zones is a layer of somewhat flattened cells, with specially thin walls, which have sometimes broken down.

The explanation which we propose for this structure is, that the inner zone is true phloëm, formed directly by the cambium on its exterior surface, while the outer layers, with thicker cell-walls, constitute an internal periderm. The intermediate flattened layer would, in this case, be the phellogen, which must have arisen by the division of cells themselves belonging to the secondary phloëm-parenchyma. This explanation also applies well to the other preparations in which the secondary cortical tissues are shown, though the carbonaceous contents of the inner layers are not always present.

Longitudinal sections show that the periderm consisted of short cells, in very regular series, while the inner tissue, presumably phloëm, was composed of much longer elements, possibly the sieve-tubes.‡ In some specimens (see photograph 22) the phloëm-elements are less regularly arranged than those of the periderm.

The development of periderm seems never to have been external, but to have started, from the first, in deeply-seated tissues. A good example of its first forma-

* It is convenient to use the general term "secondary cortex" for all secondary tissues external to the wood. (July 15, 1894.)

† The thickness of the secondary cortical tissues is very unequal at different parts of the circumference of the stem. It often, but not always, shows a maximum opposite each of the three protoxylem groups.

‡ See WILLIAMSON, "Organization," Part V., Plate 1, fig. 7.

tion is shown in a specimen previously figured,* in which a zone of radially arranged tissue, thin-walled at its inner edge, intervenes between the wood and the primary cortex. It is probable that this peridermal tissue arose from the division of cells belonging to the pericycle. At any rate, the whole of the primary cortex, lying outside this first-formed periderm, soon perished. Its remains, in various stages of disorganization, are found surrounding many of the more advanced stems (see, for example, Plate 83, fig. 40, where only a part of the primary cortex is represented).

Soon, however, the original periderm was itself replaced by more internal layers, arising, as we have seen, from the secondary phloëm-parenchyma. The oldest specimens had a regular scale-bark, formed by successive incomplete layers of periderm, cutting more and more deeply into the secondary cortical tissues (see photographs 22, and more especially 23, on Plate 75). At some places as many as five distinct peridermal masses can be traced, one outside the other. Each of these masses consists of thick-walled cells towards its external side, and of very regularly arranged thin-walled tissue, towards its inner margin.

Before leaving *Sphenophyllum plurifoliatum* we will return for a moment to the subject of the cambium, in order to consider the question of its first origin. We very constantly find an irregular layer of comparatively thin-walled tissue, between the concave sides of the primary xylem-strand, and the first layer of interfascicular secondary wood (see especially Plate 75, photograph 20, and Plate 83, fig. 40). At the angles of the primary xylem on the other hand, the first secondary tracheæ appear to abut directly on those of the protoxylem (see also photograph 19 and fig. 43). We may infer then that the *fascicular* cambium (in the sense above explained) arose from the first parenchymatous layer immediately adjoining the protoxylem, while the *interfascicular* cambium at its first origin was separated from the central wood by at least one layer of permanently parenchymatous cells.

It is probable that the formation of secondary wood always began in the interfascicular region.† Sometimes it extended at once round the protoxylem-angles; in other cases the completion of the ring was delayed, so that we may even find three layers of interfascicular wood, while no trace of secondary tissue has as yet appeared opposite the groups of protoxylem.

2. Sphenophyllum insigne, nobis.

This is the species originally described under the name of *Asterophyllites insignis*,‡ and includes all the specimens of *Sphenophyllum*, showing structure, received from Burntisland. At the time when the fossil was first described, nothing was known of

* C.N. 874, Williamson, *loc. cit.*, Part V., Plate 3, fig. 16.

† See Williamson, *loc. cit.*, Part V., Plate 1, fig. 2. (C.N. 872.)

‡ Williamson, "Organization," Part V., 1873.

its foliage. Now we are in a somewhat better position, though our information on this subject is still imperfect.

One of the most important of the additional specimens is that of which a part is represented, in longitudinal section, in Plate 84, fig. 47. This section passes through a node, which is very clearly shown, and corresponds well with the nodes of other species of *Sphenophyllum*. On both sides the bases of the leaves are evident. Below these the cortex is dilated for some distance. The vascular bundles appear to have passed out obliquely; on one side the outgoing tracheæ could be seen. The identity of this specimen with the other Burntisland examples of *Sphenophyllum* is sufficiently proved by the structure of the secondary wood. If fig. 47B, which is taken from the specimen with the node, be compared with fig. 50, which is taken from one of the largest specimens, the agreement in structure is manifest, the peculiar medullary rays being especially characteristic.

We have another preparation which shows something of the leaves. This is an approximately transverse section of a very young stem (see Plate 83, fig. 46). A part of the whorl of leaves is shown, with two vascular bundles passing out through it. Judging from this specimen, the leaves in each verticil could not have been very numerous; probably not more than six. They were evidently coherent for some distance from their base.

Primary Structure.

The primary structure of the stem of *S. insigne* is on the whole similar to that of *S. plurifoliatum*. The cortex of the young stem has the same characteristic form as seen in transverse section. There is a marked depression opposite each of the concave sides of the triarch strand of wood (see Plate 76, photograph 23; Plate 83, fig. 45).

The primary xylem agrees in general anatomical features with that of the former species. Here also the triquetrous strand of tracheæ is quite solid, and destitute of parenchymatous elements of any kind. The tracheæ are of smaller size than those of *S. plurifoliatum*. Towards the middle of the strand they are pitted; their pits are very variable in form; sometimes they are oval, and not unlike those of the former species; often, however, they are more transversely elongated, and approach the scalariform type. Towards the angles of the strand the elements become rapidly smaller; at each corner there is constantly an intercellular space or canal, which affords a good distinctive character from *S. plurifoliatum,* in which such canals are never found (Plate 76, photograph 23; Plate 83, fig. 45). Surrounding the canal are spiral tracheæ, which are much more frequent here than in the last species. Fragments of spirals are also often found in the canal itself (see Plate 85, fig. 53).

It would be rash to assume that the canals existed, as such, during life. It is possible that they may represent the position of thin-walled tissue which accmopanied the spiral elements. It is, however, equally likely that they were actual lacunæ,

formed by the rupture of the tissues, as so often happens in similar positions. The numerous, often uncoiled spiral tracheæ, at the angles of the primary xylem, are an indication that growth was still in active progress when the differentiation of the tissues began. Spirals are comparatively rare in *S. plurifoliatum*, a fact which harmonizes well with the absence of canals in that species.

There can be no doubt that in *S. insigne*, as in other species, the primary xylem was triarch and centripetal, the three peripheral groups of spiral tracheæ marking the three points at which differentiation started. We cannot see any proof that there were two groups of protoxylem at each angle. It might indeed be possible to consider the canal as separating the two arms of a crescentic group of primitive tracheæ, as is so conspicuously the case in the Autun species (see Plate 76, photograph 24). But the fact that we have repeatedly found spiral tracheæ immediately to the *outside* of the canal (see Plate 85, fig. 53) appears to us to negative such a view, and to prove that the protoxylem at each angle was a single group.

As regards the other primary tissues there is little to detain us. The inner cortical layers, which cannot be distinguished from the pericycle and phloëm, were thin-walled, and are very imperfectly preserved in the less advanced specimens. We can therefore give no information as to the *primary* phloëm, though we shall find that the *secondary* phloëm was well preserved in some of the older stems.

The outer cortex consisted of somewhat thick-walled tissue, but less sclerotic than that of *S. plurifoliatum*. The cells which, in the internodes, are of considerable length, were generally parenchymatous in form (Plate 84, fig. 47).

As regards the course of the leaf-trace bundles, it appears probable from the preparation shown in Plate 83, fig. 46, that two foliar bundles were given off from each angle of the triarch stele.

For the mode of *branching*, we have only the evidence of one specimen,* the interpretation of which is doubtful. We shall return to the consideration of this specimen, after describing the secondary tissues.

Secondary Changes.

The development of secondary wood and phloëm and of periderm proceeded in *Sphenophyllum insigne* in the same general manner as in *S. plurifoliatum* and other species of the genus. The structure of the secondary tissues, especially of the wood, differs in some respects from that in any other species at present investigated.

As regards the largest specimens of *S. insigne*, certain authors have expressed doubt or disbelief as to their belonging to *Sphenophyllum* at all, and have supposed them to be roots, either of a Cycad, or of some unknown plant.†

* C.N. 926; see WILLIAMSON, "Organization," Part V., Plate 5, fig. 27.

† *E.g.*, RENAULT, 'Cours de Botanique Fossile,' vol. 4., p. 12 (1885); SCHENK, "Die Fossilen Pflanzenreste," in 'Handbuch der Botanik,' Bd. 4, p. 103; SOLMS, 'Fossil Botany,' p. 349.

These doubts, as we shall proceed to show, are groundless. We have a series of specimens with secondary wood of all thicknesses up to 36 elements in each radial series. The smaller of these specimens (such as that shown in the photograph 23, on Plate 76) still retain the characteristic primary cortex, and no doubts have been, or can be, entertained as to their nature. Their structure, however, already presents the same peculiarities which have given rise to suspicions in the case of the larger specimens. The latter only differ from the former in the greater bulk of their secondary tissues and in the loss of their primary cortex, which is cast off in *S. insigne* exactly as in other species of the genus.

If we first consider one of the moderately thickened specimens (such as that shown in photograph 23), we find that the primary triarch wood has the structure already described (*cf.* fig. 45 on Plate 83). Upon this primary strand several layers (7–10 in the specimen photographed) of secondary xylem have been deposited. This tissue is thickest opposite the middle of each of the three concave sides of the primary wood, and thins out considerably towards its angles. The xylem elements are arranged with characteristic regularity in radial series. The distinction between fascicular and inter-fascicular wood is already well marked.

There are, however, two distinctive characters presented by this wood as compared with that of the other species.

(1.) The tracheæ have scalariform markings, at least on their radial walls. This is shown very plainly, both in oblique sections* and in the longitudinal section already referred to (C.N. 1420, see Plate 84, fig. 47). The tangential walls do not generally show any pits; when present on these walls the pits are small and rounded.

(2.) The more striking difference consists in the presence, in all parts of the wood, of regular medullary rays, one or two cells in breadth, extending through the whole thickness of the secondary zone. Occasionally isolated cells occur at the corners of the tracheæ, but, as a rule, the parenchyma of the wood takes the form of continuous rays. Comparison with a longitudinal section (see Plate 83, fig. 47B) shows that these rays may be one cell in height or more. Their elements have a lenticular form, as seen in tangential sections of the stem.

The primary cortex is well preserved in these younger specimens (see photograph 23). A zone of secondary tissue, no doubt including both phloëm and periderm, surrounds the wood; its structure is more evident in the more advanced specimens.

Other examples, with secondary wood from 11 to 22 elements in radial thickness, show precisely the same structure.†

Here, however, the secondary cortical tissues have reached a considerable thickness, and their cells are in regular radial series. Outside this zone the remains of the primary cortex can still be traced.‡

* As in C.N. 910.

† For the details of the wood, see Plate 84, figs. 49–52, and compare with the structure of the younger stem shown in fig. 47.

‡ C.N. 922 and 926.

Lastly, we have the largest specimen, figured in transverse section by WILLIAMSON,* the identity of which has been disputed.

The primary xylem in this specimen has exactly the same structure as in the smaller stems; the canals at the angles, containing fragments of spiral tracheides, are perfectly evident. The secondary wood, which reaches a maximum thickness of 36 elements, agrees in every respect with that of the less advanced specimens; the medullary rays are alike, and so are the tracheæ, with their scalariform radial walls.† In fact, if the more central portion of the largest specimen were seen alone, it could not be distinguished from the corresponding region of one of the younger stems, which still retain the typical cortex of a *Sphenophyllum*.

In the most advanced specimens the primary cortex has, as we should expect, entirely disappeared; it is replaced by an enormously thick bark, formed by successive layers of internal periderm (see Plate 84, figs. 48, 51, and 52).

We maintain, then, that there is no longer the slightest reason to doubt that the largest, as well as the smallest, specimens under consideration belong to one and the same species, namely, to that species of the genus *Sphenophyllum* to which we give the name of *S. insigne*.

The sections in which no primary cortex is shown would, *by themselves*, suggest to any botanist the idea of a root. The root-like anatomy, however, is common to all specimens of the genus *Sphenophyllum*, and is no more remarkable in a large stem than in a small one. The comparison of specimens of various dimensions shows that the only change consists in the formation of additional secondary layers, and in the casting off of the primary cortex, owing to the development of internal periderm.

The presence of true medullary rays in all parts of the wood is certainly exceptional in *Sphenophyllum*, so far as our present knowledge extends. This peculiarity, however, is not confined to the larger specimens of *S. insigne*, but is already present in stems which still retain the unmistakeable cortex and node of a *Sphenophyllum*.

Of the details of structure of the secondary wood little remains to be said. The medullary rays vary much in height. Many consist of a single series of cells, others of two series; in extreme cases even as many as 15 rows may be superposed to form a single ray. The larger rays are usually two or more cells in breadth in some parts. The uniseriate rays, as seen in radial section, are perfectly similar to the radially-elongated cells of *S. plurifoliatum*, except that in *S. insigne* these cells lie in one and the same straight line (compare Plate 83, fig. 44, and Plate 84, fig. 49). The importance of this difference is not to be underrated. It probably indicates a different mode of development from the cambium. We must, however, remember that even in

* *Loc. cit.*, Part V., Plate 4, fig. 21.

† Our figures 48, 49, 51, and 52 (all on Plate 84), are from this largest specimen. The figures in WILLIAMSON, *loc. cit.*, Part V., Plate 4, should also be compared. Our figures 47, 50, and Plate 85, fig. 53, are from smaller stems.

S. plurifoliatum continuous rays do occur, more especially in the fascicular part of the wood,* so the distinction is by no means an absolute one.

The pitting of the tracheæ is often beautifully preserved; in tangential sections it is evident that the scalariform pits were bordered (Plate 84, fig. 50). On the surface of junction of tracheæ and ray-cells the border is unilateral.

Whether the tracheæ were true vessels or tracheides can hardly be determined. If they were tracheides they must have been of great length, for they can often be traced all through a section without finding any terminal wall. In some cases, however, we have observed, in tangential sections, what appear to be the very tapering ends of tracheæ. We do not regard this observation as decisive, for such appearances might possibly be due to slight obliquity of the section. The question must therefore be left open. Now that the transverse lines seen in radial sections have been proved to represent the walls of cells external to the tracheæ, there is no longer any evidence for the existence of transverse septa in the latter.

The cambium appears to have originated in exactly the same position in this species as in *S. plurifoliatum*.

Appearances suggestive of annual rings are sometimes met with in *S. insigne*, but the same remarks apply here as in the case of the former species.

In a longitudinal section of the largest stem† a protoxylem-canal is shown, which is partly blocked up by polygonal cells. As the canals are empty in the younger specimens, it is probable that these cells were of the nature of *thyloses*.

It remains to consider the secondary tissues external to the wood. In the more advanced specimens (see Plate 84, fig. 48) the thick cortical zone‡ is composed of radially arranged cells. Their radial series correspond with, but are usually more numerous than, those of the wood. The walls of the cortical cells become thicker towards the exterior. The limit between phloëm and internal periderm is not always obvious. In favourable cases, however, where the delicate phloëm happens to be particularly well preserved, or where, perhaps, it was developed in unusual amount, the whole structure is clear. This is the case, for example, in the largest specimen, of which corresponding transverse and radial sections are shown in Plate 84, figs. 51 and 52. Adjoining the wood we see evident remains of the tabular cambial cells. Outside these we find a group of thin-walled tissue, in which the arrangement of the cells, though somewhat irregular, shows traces of a radial seriation. Some of the cells in this group are of large size, in fact not much smaller than the tracheæ of the wood. Beyond these, again, are flat, thin-walled cells, passing over on the outside into thicker-walled periderm, only a small part of which is represented in fig. 51. If we compare the radial section with this the corresponding parts are evident. The

* This seems to be also the case in the Autun *Sphenophyllum*. See RENAULT, 'Cours de Bot. Fossile,' vol. 4, plate A, fig. 4, *r*.

† C.N. 924.

‡ *Cf.* foot-note above, on p. 925.

outer limit of the wood is sharply defined; next comes a layer of excessively delicate, elongated cells, doubtless the cambium. Further to the exterior we find a zone of long, thin-walled elements, some of which are of considerable diameter, and are somewhat dilated at the transverse septa. These evidently correspond to the large, thin-walled cells of the transverse section. The resemblance of these elements to the sieve-tubes of the higher plants is very striking, nor are sieve-tubes of similar form unknown among the vascular Cryptogams. In *Marattia*, for example, they are sometimes quite of this type. We think it quite possible that these elements in *Sphenophyllum insigne* may really have been of the nature of sieve-tubes.

Still further towards the outside we find the very regular, short-celled periderm; its inner cells have thin walls, and no doubt represent the phellogen. The gap in the figure, separating the periderm from the phloëm, is merely a local lesion, for, in other parts of the same section, all the tissues are continuous.

From the study of the transverse section, as a whole, it appears that the phloëm was not equally developed all round the stem, but was specially localized at certain points.

The periderm attained a great thickness; in the largest specimen four distinct zones can be recognized, so that here, as in *S. plurifoliatum*, there was evidently a repeated formation of phellogen in successively deeper-seated layers. This great development of internal periderm, and consequent throwing-off of the whole primary cortex, seems to have been a striking characteristic of the genus.

Before concluding our account of this species we will return to a specimen, already referred to, which shows the base of a lateral appendage. The section in question* is an incomplete transverse one, showing only one angle of the primary wood. About ten layers of secondary wood are present, and both primary and secondary cortex are fairly preserved. Opposite the protoxylem-group a large bundle of scalariform or reticulated tracheæ, accompanied by parenchyma, runs out in an horizontal direction. The outgoing strand is too large for a leaf-trace; it must have belonged either to a branch or an adventitious root. The cortex appears to be ruptured at the exit of the strand. On the whole, we are inclined to regard the appendage as a root, for its origin seems to have been endogenous. No certain conclusions, however, can be drawn from this isolated specimen.

To sum up, we find that the chief anatomical characteristics of *Sphenophyllum insigne*, are the following:

1. The presence of a canal at each angle of the primary triarch xylem.
2. The scalariform thickening of the secondary tracheæ, at least as regards their radial walls.
3. The presence, throughout the secondary wood, of continuous medullary rays.

* C.N. 926 (see WILLIAMSON, *loc. cit.*, Part V., Plate 5, fig. 27).

4. The occurrence of very large elements, resembling sieve-tubes, in the phloëm-region.

These characters are sufficient to differentiate the species. In the arrangement of the leaves, the outline and structure of the primary cortex, the centripetal triarch xylem, and the mode of growth in thickness, the plant is a typical *Sphenophyllum*, in which genus it finds its natural resting-place.

THE FRUCTIFICATION OF SPHENOPHYLLUM.

SPHENOPHYLLUM DAWSONI, NOBIS.

The fructification which we are about to consider was first described in 1871, under the name of *Volkmannia Dawsoni*, unless, indeed, as M. ZEILLER suspects, the plant described by BINNEY, in the previous year, as *Bowmanites cambrensis*, be the same species.*

Further accounts of the same fossil were published in 1873 and 1890, and, in 1891, a very complete description was given of its structure, on the basis of a number of newly-discovered specimens.†

In 1884 the species was placed by WEISS in BINNEY'S genus *Bowmanites*,‡ a view which was accepted in the later memoirs of WILLIAMSON.

In 1892, M. ZEILLER§ communicated to the French Academy the results of his examination of some extremely fine fructifying specimens of *Sphenophyllum cuneifolium*, STERNB., from the French and Belgian Coal-Measures. He expressed himself as convinced of the complete identity of WILLIAMSON'S specimens of *Bowmanites Dawsoni*, with the fructifications of his *Sphenophyllum*.||

This year (1893) M. ZEILLER has published his work in full.¶ His detailed descriptions, and especially his beautiful photographic illustrations, leave no doubt as to the essential agreement between the undoubted strobili of *Sphenophyllum*, which he investigated, and the English specimens described as *Bowmanites Dawsoni*. The question of *specific* identity of the latter with *Sphenophyllum cuneifolium*, is one which we prefer to leave open for the present. One of us (D. H. SCOTT) has had the

* WILLIAMSON, "On the Organization of *Volkmannia Dawsoni*," 'Mem. Lit. and Phil. Soc. of Manchester,' Ser. 3, vol. 5; BINNEY, "Observations on the Structure of Fossil Plants," Part 2, 'Palæontographical Society,' volume for 1870.

† WILLIAMSON, "Organization of Fossil Plants of the Coal-Measures," Part V. (1873); Part 17 (1890); and Part 18 (1891); 'Phil. Trans.'

‡ WEISS, 'Steinkohlen-Calamarien,' vol. 2, p. 200.

§ 'Comptes Rendus,' vol. 115, July 11, 1892.

|| This conclusion has already been provisionally accepted by WILLIAMSON, 'Nature,' vol. 47, Nov. 3, 1892.

¶ "Etude sur la constitution de l'appareil fructificateur des Sphénophyllum," 'Mém. de la Soc. Géol. de France; Paléontologie,' Mém. 11, 1893.

opportunity, through the kindness of M. ZEILLER, of thoroughly examining his original specimens, and was able completely to confirm his conclusions.

We propose first to give a general account of the organization of the strobilus, as shown in the English specimens, in which alone the internal structure is preserved. The facts already known will be briefly recapitulated, while some additional points of interest, which have been revealed by our renewed examination of the specimens, will be described more fully. Finally, we shall state the reasons which have induced us to accept M. ZEILLER's conclusion that this strobilus is the fructification of a *Sphenophyllum*.

For the present we propose to retain the specific name originally given to the English specimens, which we shall therefore describe as *Sphenophyllum Dawsoni*.

General Morphology.

The strobilus consists of a somewhat slender axis (attaining 2·5 millims. in diameter) bearing a number of successive verticils of coherent bracts. The largest number of whorls preserved in any of our specimens is 8 (in C.N. 1898 K, part of which is represented in Plate 85, fig. 54); the total number was no doubt much greater.

The coherent portion of the bracts, forming the *disc* of previous memoirs, extended for a distance about equal to the diameter of the axis. It then divided up into the free bracts, or "disc-rays." The latter had a somewhat lanceolate form, broadening out for some distance from the base, and then tapering again towards the apex. On leaving the axis the bracts take an obliquely upward course, curving rapidly towards the apex of the strobilus, until their direction is nearly vertical (Plate 85, fig. 54). The free limbs of the bracts were of great length, as is shown by the fact that in transverse sections we may find as many as six overlapping whorls, proving that the extreme vertical length of the bracts must sometimes have been equal to about six internodes, giving an extreme absolute length of perhaps 12 millims.*

The number of bracts in a verticil could not be determined with certainty; apparently it was about fourteen in some of the smaller specimens, and not less than twenty in the larger.

From the position of the overlapping tips it appears that the bracts of successive whorls alternated with one another. This is somewhat surprising, for the leaves in the vegetative verticils of *Sphenophyllum* were superposed. This is, however, no argument against the identification of our specimens with *Sphenophyllum*, for in M. ZEILLER's strobili, borne on the stems of typical *Sphenophyllum crucifolium*, the alternation of the bracts is still more evident.

The sporangia are not borne directly on the bracts, but each is seated on the end of a long pedicel or sporangiophore. The pedicels are twice as numerous as the bracts;

* M. ZEILLER's estimate, based on the figures of Memoir XVIII., is 8 millims. Some of his specimens of *S. cuneifolium* have bracts 10–13 millims. in length. See his Memoir above cited, p. 21.

they arise from the upper surface of the coherent disc near the axil. The extent to which they adhere to the surface of the disc varies greatly; in some cases they become free at once; in others they do not become wholly free until the point is reached where the bracts themselves begin to separate from one another.* It does not appear, however, that there was ever more than a single verticil of sporangiophores belonging to each verticil of bracts; appearances to the contrary seem to be due to the varying degree of adhesion between the two organs (Plate 85, fig. 54).

A transverse section of the strobilus may show one or two circles of sporangia between two whorls of bracts; sometimes even a part of a third circle is present. The same variations are observable in tangential sections. These differences can only be explained by the fact that the sporangiophores overlap each other, so as to bring their sporangia to different levels. Where additional sporangia appear within the same internode, their position is both *exterior* and *superior* to those of the first circle (see Plate 76, photographs 25 and 26, and compare with the figures in WILLIAMSON, Part XVIII.). Hence the longer pedicels must have passed to the outside of the sporangia borne on the shorter ones, as is often well shown both in transverse and tangential sections.†

The longer sporangiophores considerably exceed an internode in length, for we find sporangia belonging to two successive verticils of bracts appearing in the same transverse section.‡

The sporangiophores follow the upward curvation of the bracts, keeping at a little distance from their superior surface. Each bears at its end a single sporangium, which is attached in a very characteristic manner. The pedicel bends inwards at its extreme end, and the sporangium is suspended from it, so as to hang almost parallel to the pedicel, occupying a position rather like that of an anatropous ovule in relation to its funicle (Plate 76, photograph 25; Plate 85, figs. 57 and 58).

This short account of the general morphology of the strobilus may suffice as an introduction, considering the full descriptions which have already been published. We will now proceed to consider its internal structure.

The Axis.

The axis of the strobilus is traversed by a solid vascular cylinder, of which only the wood retains its structure. In the larger specimens the wood forms a very bluntly triquetrous strand.§

Each of the obtuse corners is prolonged into two projecting points, with a marked bay between them. The smallest tracheæ are at the points, so that we may

* See WILLIAMSON, "Organization," Part V., Plate 5, fig. 28; Part XVIII., Plate 26, fig. 7.

† WILLIAMSON, *loc. cit.*, Part XVIII., Plate 26, fig. 2; and Plate 25, fig. 8.

‡ WILLIAMSON, *loc. cit.*, Part V., Plate 5, fig. 28.

§ See WILLIAMSON, *loc. cit.*, Part V., Plate 5, fig. 29; and Part XVIII., Plate 25, fig. 1.

reasonably assume that in this case there were six distinct groups of protoxylem, as in some of the species of *Sphenophyllum* investigated by M. RENAULT (see Plate 76, photograph 24, from the Autun form). It is noticeable that the whole periphery of the woody mass is occupied by elements decidedly smaller than those of the interior. There is not the slightest indication of a pith, or of any parenchymatous cells among the thick-walled tracheæ. Longitudinal sections show tracheæ only, the larger of which appear to have pitted walls. One section (see Plate 85, fig. 54) which probably passed through the xylem near one of its angles, also shows scalariform and spiral tracheæ; the latter are small and no doubt represent the protoxylem.

The soft tissues surrounding the wood have entirely perished, except for a mere structureless film, which, in one specimen, extends between the angles of the wood.

In one of the smaller specimens (see Plate 86, photograph 26) the xylem-strand is excessively slender, and its angles acute, though here also there are some indications of a double group of protoxylem at each. It is doubtful whether these small specimens are identical with the larger ones, which have a massive strand of xylem. It is possible that they may belong to a second species, but we have not sufficient evidence to justify their separation. The spores of the larger and smaller strobili show no constant difference in size.

The specimen from which fig. 54 is drawn, evidently belongs to the smaller form; the diameter of the whole strobilus is only about 6 millims., while those of the larger type are on the average at least 12 millims. in diameter.

The outer cortex of the axis is well preserved. Its inner cells are thin-walled and parenchymatous, but towards the exterior they have thicker walls and are more prosenchymatous in form.

As regards the course of the leaf-trace bundles running out into the bracts, our data are incomplete. None of our sections show the out-going bundles at the point where they diverge from the central cylinder. On the other hand we have some excellent preparations showing the bundles in the outer part of their course. In several sections we see them just at the inner edge of the cortex, or rather of that outer zone of cortex which is alone preserved.* The bundles in this position are of considerable size, and may contain as many as twenty tracheæ. Their smaller elements are towards the exterior, and are spirally thickened, while the inner and larger tracheæ are scalariform, or at least their spiral band is more closely coiled. These facts can be made out where the section is oblique. We may infer then, that the xylem of the leaf-trace bundle was *centripetal.*

The bundles which we meet with in the cortex are often larger than those which pass out into the whorl of bracts, and no doubt sometimes subdivided on their way through the outer cortical layers.

* See WILLIAMSON, *loc. cit.*, Part XVIII., Plate 27, fig. 3. They are also well shown, on a small scale, in our photograph 25, on Plate 76.

The Bracts.

In transverse sections passing through the base of the disc, or coherent whorl of bracts, we find the out-going bundles again, just where they leave the cortex, and pass out obliquely into the verticil (see Plate 85, fig. 55, which is from the same section as the more general figure in WILLIAMSON, Part XVIII., Plate 27, fig. 9).

At this point each bundle undergoes a division into three. One branch, the most external of the trio, continues its course through the disc; the two others are given off on the inner side, towards the axis, *and supply two sporangiophores* (compare figs. 55 and 56, on Plate 85). The external branch in each case runs straight out through the disc into one of the free bracts, each of which always contains a slender vascular bundle, a fact which has been previously overlooked.

The bundle-system of the appendages then, is clear; each bract receives a single bundle from the axis; immediately on entering the verticil the bundle gives off two branches in an upward and inward direction. These branches constitute the bundles of the two sporangiophores corresponding to the bract in question. The determination of this fact supplies the answer to a question raised by M. ZEILLER in his memoir above cited,* as to the relation between bracts and sporangiophores. The anatomy, as well as the external morphology, indicates plainly that the sporangiophores are appendages of the bracts, and not independent outgrowths of the axis.

As regards the structure of the bracts, a few words will suffice. In the coherent portion of the whorl the parenchyma is, on the whole, very uniform, except that we find a palisade-like layer near the insertion of the whorl and towards the lower surface (Plate 85, fig. 54). The xylem of each vascular bundle is surrounded by an empty space, which no doubt marks the position of the phloëm and thin-walled tissue. It is not possible to determine whether the bundle was collateral or concentric.

The free bracts have a well preserved epidermis, in which smaller cells are seen here and there, but no definite stomata can be detected. Usually only the middle part of the mesophyll is preserved; towards the edges of the bract the space within the epidermis is empty. Through the middle of the persistent central tissue runs the slender vascular bundle, which can only be well seen in the most favourable sections. In other respects, a previous figure gives a sufficient idea of the structure.†

The Sporangiophores and Sporangia.

The insertion of the sporangiophores, as determined by the point at which their vascular bundles are given off from those of the bracts, appears to be constant, while the amount of adhesion, beyond this point, between the sporangiophores and the coherent disc, is very variable, as has already been explained.

* *Loc. cit.* p. 21.

† WILLIAMSON, *loc. cit.*, Part XVIII., Plate 27, fig. 12.

The sporangiophore, in its lower part, is a small cylindrical pedicel, of simple structure. Its diameter near the base is only about ·15 millim. It has a well-marked epidermis, beneath which there is sometimes a rather sclerotic hypodermal layer.* The delicate inner tissue is more or less disorganized. The xylem of the vascular bundle, which here consists of two or three tracheæ only, is placed towards the adaxial surface.

As we follow the sporangiophore upwards, we find a gradual change in its structure. Certain of the epidermal cells become enlarged. Sometimes one cell on each side projects beyond its neighbours, giving a winged appearance to the transverse section. As we approach the sporangium, the sporangiophore grows thicker, attaining a diameter of about ·4 millim. In this part all the epidermal cells of its outer or dorsal surface are enlarged. The transverse section is here approximately semi-circular (see Plate 85, fig. 57). The vascular bundle contains many more tracheæ than in its lower part; we can now see clearly that while the xylem, as a whole, is situated towards the inner surface (an indication that the bundle was collateral), its smallest tracheæ are directed outwards. This is constantly the case wherever the preservation permits the structure to be clearly seen. It appears then that in the sporangiophore, as in the leaf, the xylem was *centripetal.* All the tracheæ are spiral.

The sporangiophore bends over at its extremity, towards the axis of the strobilus. Here the sporangium is attached to it with a fairly broad base. The xylem preserves its full thickness to the last, and comes to a sudden end, being obliquely truncated where the cavity of the sporangium begins. The thin-walled tissue surrounding the xylem extends further into the sporangium, and gradually thins out along its walls (see Plate 85, fig. 58; Plate 76, photograph 25, and more especially WILLIAMSON, Part XVIII, Plate 27, fig. 16).

The sporangium, as already mentioned, lies back nearly parallel with the pedicel, with the flat side of which it is in contact (figs. 57 and 58).

In our specimens the wall of the sporangium is but one cell in thickness, except near the base. The wall is similar in structure to the epidermis of the adjoining portion of the sporangiophore. M. ZEILLER has suggested several questions as to the sporangial wall, which we have endeavoured to solve.† He enquires whether there is a regular diminution in the size of the cells of the wall, as the distance from the pedicel increases. There is certainly a diminution, but it is not quite regular. We often find a constriction near the base of the sporangium, which we may take as marking the limit between the sporangial wall and the epidermis of the pedicel (see photograph 25, and figures above cited). Beyond this constriction, large cells, just like those of the epidermis, recommence. They gradually diminish in size, as we trace the sporangial wall towards the free end, but soon their diameter becomes uniform.

* WILLIAMSON, *loc. cit.*, Part XVIII., Plate 28, fig. 15.

† *Loc. cit.* p. 22.

Quite at the end of the sporangium, however, we often find a group of specially narrow cells, suggesting that here dehiscence took place. Measurements give the following average results :—

Large epidermal cells of pedicel	·12	millim. radial diameter.
Largest cells of sporangial wall	·12	,, ,, ,,
Ordinary cells of wall	·073	,, ,, ,,
Narrowest cells of wall	·036	,, ,, ,,

What has just been said answers another of M. ZEILLER's enquires (*loc. cit.* p. 23), namely, whether the largest cells belong exclusively to the pedicel, or whether some also belong to the sporangium itself. Undoubtedly the latter is the case.

A third point suggested by M. ZEILLER for investigation relates to the thickening of the membranes of the large cells in question. He compares them to the annulus in Ferns, and enquires whether, like the cells of that organ, they are more thickened on their inner than on their outer surface. We have carefully examined the cells both of the pedicel, and of the sporangial wall, from this point of view. They are quite similar to each other, and their membranes show a distinct thickening in the form of bars, running along their lateral walls in the radial direction. In some cases the thickened ridges extend also over the inner and outer cell-walls, but we could detect no difference between them as to thickness.

The Spores.

The spores of *Sphenophyllum Dawsoni* are already well known; their cell-wall possesses a highly characteristic ornamentation, consisting of prominent spines, which are connected together on the external surface of the exosporium, by a reticulum of elevated ridges.* This structure is quite constant; in one strobilus only did we find any deviation from it. In this specimen only two of the sporangia shown in the section† contain typical spores, which are here about ·1 millim. in diameter. The other sporangia contain thin-walled spores, without spines, and of somewhat smaller size, though not smaller than the typical spores of some other specimens. It is probable that the thin-walled spores in this strobilus were immature.

There is nothing whatever, in any of our specimens, to suggest that the fructification was heterosporous. As about a dozen distinct specimens have now been examined, it is highly probable that if two kinds of spores were present, both must have been observed. The variations in the size of the spores are inconsiderable, ·076 millim. to ·104 millim. being the extreme range; these extremes are connected by spores of intermediate dimensions.

* See WILLIAMSON, *loc. cit.*, Part XVIII., Plate 25, figs. 17 and 18. See also our own figures 57 and 58, on Plate 85.

† C.N. 1049 C, figured by WILLIAMSON, *loc. cit.*, Part XVIII., Plate 28, fig. 6.

The Vegetative Stem.

A specimen which appears to throw light on the structure of the stem of this plant in its vegetative region, has been described and figured in a previous memoir.* This specimen is a mere fragment, of which we know only the transverse section. It was obtained from the same source, the Foot-mine at Oldham, which has yielded some of the specimens of the strobilus itself.

The primary wood is bluntly triquetrous, and appears to consist of a perfectly solid mass of tracheæ. The details of its structure, so far as the transverse section can show, are absolutely identical with those of the xylem-strand in the axis of the strobilus.†

In the vegetative specimen, however, the primary xylem is surrounded by a zone of secondary wood, 12–15 elements in thickness. The structure of this secondary wood agrees exactly with that of *Sphenophyllum plurifoliatum*, except that the distinction between fascicular and interfascicular wood is somewhat less marked than in that species.

Portions of the secondary cortex are also preserved ; the cortical cells are arranged in radial series, which generally correspond to those of the wood. At one place we could distinguish three zones of cortical tissue.‡ It is probable that we have in this stem, as in the species of *Sphenophyllum* above described, a succession of deep-seated peridermal layers.

So far as the evidence extends, there is every reason to suppose that this specimen is a stem of the same plant as that to which the strobilus belonged. It differs from the axis of the latter just in those points (secondary thickening, and loss of primary cortex) in which we should expect a persistent vegetative stem to differ from the short-lived axis of a fructification. The primary structure of the two, so far as it can be compared, is identical.

Now the anatomy of the vegetative specimen is that of a *Sphenophyllum*, though somewhat different from that of any of the species of which the structure has been previously described. This specimen thus established a presumption that "*Bowmanites Dawsoni*" was the fructification of a *Sphenophyllum*, or of some closely allied plant. This presumption has now been raised to a certainty by M. ZEILLER's observations.

AFFINITIES.

M. ZEILLER's investigation of his fine specimens of the fructification of *Sphenophyllum cuneifolium* has established the following facts : the bracts of each verticil

* WILLIAMSON, "Organization," Part XVII., Plate 15, fig. 19.

† Compare WILLIAMSON, *loc. cit.*, Part XVII., Plate 15, fig. 19, with Part V., Plate 5, fig. 29, or with Part XVIII., Plate 25, fig. 1.

‡ Not clearly shown in the figure cited.

are coherent at the base, forming a funnel-shaped disc; they then become free from one another, and their free portions extend to a height equal to two or three internodes; the outline of each bract is linear-lanceolate. The sporangia are pluriseriate in each internode, being ranged in two, three, or perhaps, sometimes four circles, of increasing radius, and placed one above another. The sporangia are not attached directly to the bracts, but are borne singly at the end of filiform pedicels of varying length, which are thickened at their summit; these pedicels start from the coherent portion of the bracts, and run parallel to the latter, keeping a little above their superior surface; the pedicels become erect near their summit, and curve back towards the axis, following the external outline of the sporangium, which is attached by its superior extremity. Near the point of attachment, large cells, with more or less thickened lateral walls, can be distinguished on the dorsal surface of the pedicel, and, as it seems, on the sporangium itself.* In all these points the fructification of *Sphenophyllum cuneifolium* agrees exactly with the English specimens of *S. Dawsoni*. The only exception is that, in the latter, the bracts are sometimes of greater length relatively to the internodes.

M. ZEILLER adds a detailed comparison of the actual dimensions of his own specimens (derived from three distinct sources) with those of the English fossil; in all parts there is a most striking agreement.†

The appearance and form of the sporangium and pedicel in *S. cuneifolium* correspond exactly with our observations on the English specimens, and the same remark applies equally to the whorl of bracts.‡

The agreement in all respects is so close as to leave no doubt that the strobilus described by us is that of a *Sphenophyllum*, nearly related to, and perhaps identical with the species *S. cuneifolium*. We prefer, however, not to assume the identity of the *species* until we have some further information as to the vegetative organs of the English specimens.

Four other species of *Sphenophyllum* were examined by M. ZEILLER: *S. emarginatum*, BRONGN.; *S. gracile*, CRÉPIN.; *S. oblongifolium*, GERM. et KAULF; and an unnamed species from M. RENAULT'S collection. They all show an essential agreement with *S. cuneifolium*, especially as regards the main point, that the sporangia are borne singly on pedicels which arise from the upper surface of the bracts. In *S. oblongifolium*, M. ZEILLER was able to isolate some of the spores. Though much smaller than those of *S. Dawsoni*, they are similar in form (*loc. cit.*, p. 28).

Finally, M. ZEILLER reviews all the previous cases in which the fructification of *Sphenophyllum* has been described, and shows that all the previous observations are consistent with the presence of pedicellate sporangia rather than of sporangia borne directly on the bracts. We need not follow the details of this critical survey, but

* The above account is taken from M. ZEILLER'S summary on p. 20 of his Memoir above cited.

† See his comparative table, *loc. cit.*, p. 21.

‡ See M. ZEILLER'S figures, *loc. cit.*, Plate 1, figs. 1B and 4A; Plate 2, figs. 1A, 1B, 3A, &c.

will only call attention to one case, that of the fructification of *Sphenophyllum trichomatosum*, STUR, recently described by Mr. KIDSTON.*

The author states (p. 60) that "the oval sporangia (which have thick walls, as indicated by the amount of carbon they possess) stand upright on the bracts a short distance from their point of attachment to the cone." This statement is quite exact as regards the two sporangia to which Mr. KIDSTON is specially referring (see his fig. 1A), but from his other figures it appears that the relation of the sporangia to the bracts, and to the axis, was very inconstant. Sometimes they appear exactly in the axil, sometimes at a distance from it; in certain cases they are shown in close contact with the upper surface of the bracts, while in others they are quite separate from them. These variations would find an adequate explanation if the sporangia were borne on pedicels, which would allow of a considerable degree of displacement.

It must be remembered that the specimens of *Sphenophyllum Dawsoni* are, with two exceptions to be mentioned immediately, the only ones known in which the internal structure of the strobilus is preserved, while among the specimens in the form of impressions, those described by M. ZEILLER would appear to be by far the most perfect. The morphology of the strobilus must necessarily be interpreted in the light of those specimens in which alone it is clearly exhibited.

Two silicified fragments of fructifications, referred to *Sphenophyllum*, have been discovered by M. RENAULT. One of them has been mentioned above, and is described in M. ZEILLER's Memoir (*loc. cit.*, p. 28). Its organization agrees well with that of *S. cuneifolium* and *S. Dawsoni*. The other fragment has been interpreted by M. RENAULT as demonstrating the heterospory of *Sphenophyllum*.† M. ZEILLER has pointed out that in this specimen the sporangia were certainly borne on pedicels (*loc. cit.*, p. 34). His interpretation of the supposed macrosporangium is different from that of M. RENAULT. M. ZEILLER regards the "macrospore" as being in reality a part of the sporangial wall, while the supposed wall of the macrosporangium belongs, in his opinion, to the pedicel. One of us (D. H. SCOTT) was enabled through M. RENAULT's kindness, to examine the specimen in question, and was disposed to accept M. ZEILLER's interpretation.

Although we cannot regard the evidence derived from this specimen (which is imperfectly preserved) as by any means sufficient to establish the fact of heterospory, yet we fully allow the *possibility* that heterosporous species of *Sphenophyllum* may have existed. That both heterosporous and homosporous species may occur, within the limits of a single genus, is sufficiently proved by the case of *Calamostachys*.

The morphology of the strobilus of *Sphenophyllum* cannot be fully interpreted until the true homologies of the sporangiophores are established. Four views appear possible :—

* 'Proc. Royal Phys. Soc. of Edinburgh,' vol. 11, 1891, p. 56.

† 'Ann. des Sci. Nat., Bot.,' Sér. 6, vol. 4, 1877, p. 303, Plate 9, figs. 9–11; 'Cours de Bot. Fossile,' vol. 2, p. 102, Plate 15, figs. 7 and 8, Plate 16, fig. 3.

(1.) The sporangiophore may be a branch borne in the axil of the bracts.

(2.) It may be a leaf, which has become adherent to the whorl below.

(3.) It may be a ventral lobe of a leaf, of which the bract is the dorsal lobe.

(4.) It may simply be a sporangium-pedicel, which, unlike those of any other Cryptogam, possesses a vascular bundle of its own.

In the last case we might compare the sporangiophore with the funiculus of an ovule, but such a comparison would not advance the question much, for the true nature of the funiculus itself is still disputed.

That the sporangiophore is an axial structure, *i.e.*, a branch, does not seem to us probable. We have seen that the vascular tissue of each pair of sporangiophores is given off from the bundle of a bract, and has no direct relation to the vascular system of the axis. Further, the bundle of the sporangiophore is to all appearance a single, collateral one, a fact which would ill accord with a stem-structure.

That each sporangiophore represents an independent leaf, is a forced, though not perhaps an impossible view. We should, on this hypothesis, have to imagine a succession of alternating sterile and fertile whorls, the latter having twice as many members as the former; and we must further suppose every alternate internode to have been shortened until each fertile verticil came to be adherent to the sterile verticil next below. In the absence of any developmental data such speculations are baseless, though analogies might no doubt be found in the floral structures of certain Angiosperms. Another analogy might be traced with the Calamarian strobili. If the sporangiophores in *Equisetum* and *Calamostachys* are really leaves, as most botanists assume, then in the *Palæostachya* type, there must have been just such a shortening of the alternate internodes as is required by the hypothesis, in *Sphenophyllum.* The morphology of the Calamarieæ is, however, itself too doubtful for us to employ it in order to explain that of a remote genus.

The view that each sporangiophore is a ventral lobe of the corresponding bract is that held by M. ZEILLER,* and is perhaps the most natural of the hypotheses so far considered. In this case we must suppose each leaf to have had one dorsal lobe (the bract) and two ventral lobes (the sporangiophores). M. ZEILLER lays great stress on the analogy with *Marsilia*, and also with *Ophioglossum.* Even if we accepted these comparisons the question would be far from settled, for the morphology of *Ophioglossum*, at any rate, is itself a subject of controversy. Professor BOWER † maintains that the whole fertile spike of *Ophioglossum* is homologous with a single sporangium of *Lycopodium.* If we were to apply this view to the case of *Sphenophyllum*, we should be led back to the idea that here the sporangiophore is nothing but the stalk of a sporangium. We do not ourselves think, however, that the comparison with the complex conditions in *Ophioglossum* throws any light on the much simpler case of *Sphenophyllum.*

* *Loc. cit.*, p. 37.

† 'Proceedings of the Royal Society,' vol. 50, p. 265, 1891.

The chief objection to the simple view that the whole sporangiophore is nothing else than the pedicel of a sporangium, is the absence of any analogy among Cryptogams for such a great elongation and high differentiation of that organ. We have thought it best to state briefly the views which appear to us to be possible. We make no attempt to decide between them, and indeed regard the question as insoluble, in the absence alike of developmental facts and of satisfactory material for comparative study. We prefer to leave the whole question open, and, provisionally, to speak of the sporangiophore as a pedicel simply, without prejudging its possible homologies.

Our knowledge of the organization of *Sphenophyllum* is now fairly complete. We have not, it is true, been able ourselves to say anything as to the structure of the roots, nor to give any detailed account of the leaves. Considerable information on these points, as regards other species of the genus, will however be found in the works of M. RENAULT, cited above. But though *Sphenophyllum* is now, for a fossil plant, very thoroughly known, it still seems to us impossible to determine its affinities. That it is a vascular Cryptogam there can be no doubt, nor has this been questioned by any modern writer. Among the vascular Cryptogams, *Sphenophyllum* must rank as one of the most highly organized genera, on account both of the great histological complexity of its vegetative organs, and of the peculiar morphology of its fructification. However we may interpret the latter, it certainly has a highly specialized character. In fact *Sphenophyllum* affords yet another example of a Carboniferous Cryptogam, which, so far from representing a primitive type, is in many ways more elaborately modified than any recent forms.

It is not surprising that the most various systematic positions have been assigned to the genus by different authors. For example, SCHENK, VAN TIEGHEM, and others, have placed it near Lycopodiaceæ; STUR refers it to Calamarieæ, RENAULT to Salviniaceæ, while ZEILLER has recently traced a relationship, on the one hand, to Marsiliaceæ, and on the other to Ophioglosseæ. Mr. KIDSTON thinks that "the *Sphenophylla* form a peculiar group of plants, which, though standing close to the Lycopods, cannot be included with them, but must be placed in a class by themselves—the Sphenophylleæ."* Count SOLMS-LAUBACH also places these plants in a class of their own, thinking it best "to renounce for the present all forced attempts at classification, and to regard the group as *sui generis*, as standing by itself, and independent."† To this cautious view of the matter we give our adhesion, until additional forms shall be discovered, which may link on the genus to other families.

The chief characters which have to be taken into account, seem to us to be these: (1) the jointed axis, with superposed verticils of leaves; (2) the centripetal triarch or hexarch xylem, without a pith; (3) the structure of the strobilus, especially the mode in which the sporangia are borne, and the relation of their pedicels to the bracts.

* *Loc. cit.*, p. 61.

† 'Fossil Botany,' p. 354.

The phenomena of secondary growth, remarkable as they are, have appeared in so many diverse groups of Cryptogams and Phanerogams, that we cannot attach much systematic importance to them.

The special peculiarities of the secondary tissues in *Sphenophyllum* appear to us to have been somewhat exaggerated by previous authors. For example the absence of medullary rays, on which so much stress has been laid, does not seem to have been constant in any species, while in *S. insigne*, which we have proved to be a true *Sphenophyllum*, such rays are present in all parts of the wood. The structure of the secondary tracheæ does not seem to us to differ essentially from that in other Cryptogams with indefinite growth in thickness. Their structure has been misunderstood in the past, and represented as much more peculiar than it really is. The question whether these elements are vessels or tracheides must, indeed, be left open. Even if they are true vessels they are not without analogy among recent Cryptogams. Prof. HARVEY GIBSON has been good enough to inform us that in *Selaginella rupestris* and *oregana*, he finds perfectly typical vessels, with transverse septa which become completely perforated, only leaving an annulus to mark their position.*

The cambium of *Sphenophyllum* is perfectly normal, we might almost say typical. The most remarkable point is the repeated formation of internal layers of periderm. This has no exact parallel in other Cryptogams, though familiar enough among higher plants.

The root-like anatomy of the stem is highly characteristic, and indeed peculiar to the genus. The nearest approach to it is to be found in the centripetal xylem-strands of such Lycopods as *Psilotum* or *Tmesipteris*, with which, however, our plant has otherwise nothing in common.†

In conclusion, we must return for a moment to the fructification, in order to explain more clearly M. ZEILLER's views of its relation to that of *Marsilia* and of *Ophioglossum*. This author (*loc. cit.*, p. 37) points out the similarity between the pedicel of the sporangium in *Sphenophyllum*, and the stalk of the sporocarp in *Marsilia*. In both, the position is that of a ventral lobe of the leaf, while the mode of attachment of the sporangium in the former is similar to that of the sporocarp in the latter. We cannot, for our part, see more than a superficial resemblance here, for it seems to us impossible to compare morphologically the single sporangium of a

* Prof. GIBSON will give details in his forthcoming paper on the "Comparative Anatomy of *Selaginella*." [This has since appeared in the 'Annals of Botany,' vol. 8, number for June, 1894. July 15, 1894.]

† We cannot follow Count SOLMS-LAUBACH in his remarks on this subject. He says (*loc. cit.*, p. 354): "Assuming that the primary central bundle [in *Sphenophyllum*] belongs to the concentric type, then it may no doubt be compared with the axile strand of Lycopodieæ. But this is as yet only an assumption; the bundle might just as well be a triarch radial strand, and then there would be no resemblance to the structure of the stalk in any known living plant." We have little doubt that the central strand in *Sphenophyllum* is radial, in DE BARY'S sense, and that it is either triarch or hexarch. But surely the central strands of existing Lycopods are radial also, as DE BARY long ago showed, and as the development clearly proves.

Sphenophyllum with the elaborate sporocarp of a *Marsilia*, which is obviously a highly specialized foliar structure, containing two series of sori, with numerous sporangia in each sorus. Whatever view be taken of the *pedicel*, we see no reason to doubt that the *sporangium* of *Sphenophyllum* is simply a single sporangium and nothing more.

The comparison suggested with the Ophioglosseæ is based partly on the ventral position of the pedicel, partly on the apparently eusporangiate character of the sporangium, which could scarcely have arisen from a single cell. In order to carry out the comparison we should have to imagine the fertile spike of an *Ophioglossum* bearing a single sporangium. Here again the resemblance seems to us too remote to be suggestive of affinity.

We must be content for the present to leave this remarkable genus in its isolated position, in the hope that the extensive knowledge of its organization, which we now possess, may in the future afford an adequate basis for comparison, when additional forms of palæozoic Cryptogams shall have been brought to light.

In concluding this paper, we desire to acknowledge the essential help of those gentlemen who have contributed the illustrations.

All the drawings reproduced in Plates 77 to 85 are the work of Mr. GEORGE BREBNER, formerly Marshall Scholar in Biology at the Royal College of Science, London.

Of the micro-photographs, occupying Plates 72 to 76, the first two were taken by Professor J. B. FARMER, of the Royal College of Science, while all the rest, 24 in number, are the work of Mr. A. E. TUTTON, Demonstrator in Chemistry at the same College.

The seven photographs in Plate 86, representing medullary casts of *Calamites*, were kindly taken for us by Mr. A. GEPP, of the British Museum, Natural History Department. For the loan of these specimens for photographic purposes, we have been indebted partly to Dr. WOODWARD and partly to Mr. CARRUTHERS.

EXPLANATION OF PLATES 72–86.

PLATES 72–76.—Photographs from the actual sections. Many of the photographs need to be examined with a lens.

PLATE 72.

Calamites.

Photograph 1. Transverse section of a very young twig, corticated. Seven vascular bundles are shown, each with a large canal on its inner side. Primary structure still unchanged. C.N. 1020. × about 60. See also Plate 77, fig. 2.

Photograph 2. Transverse section of a larger branch, with 19 vascular bundles;

cortex well preserved. Several layers of secondary wood have already been formed. Outer part of the pith persistent. C.N. 1553. × about 15. See also Plate 77, fig. 3.

Photograph 3. Part of a transverse section of a larger branch, at a more advanced stage; seven of the vascular bundles (21 in all) are shown. Numerous layers of secondary wood have been formed. The cortex is differentiated into two layers. C.N. 118*. × about 25. See also Plate 78, figs. 12, 13, and 14.

Photograph 4. Radial section of part of a decorticated branch, showing two nodes, with their diaphragms. There is a considerable zone of secondary wood. Above the upper node, on the right hand, part of the base of a branch is shown. C.N. 1937. × about 9. From Mr. WILD's specimen.

Photograph 5. Tangential section through the wood of an advanced stem. The section passed through the inner part of the secondary wood. Five outgoing foliar bundles are seen in transverse section, as well as two branches out of the four which the complete section shows at this node. Observe that there is no regular alternation of the vascular bundles above and below the node. Observe the small-celled tissue of the medullary rays below the node. C.N. 130*. × about 12.

Photograph 6. Similar section of another specimen. This section has passed somewhat further towards the exterior. Several foliar bundles are shown, and one branch. Observe that its connection with the tracheæ of the main stem is chiefly from below. C.N. 1554. × about 12.

PLATE 73.

Photographs 7, 8, and 9. *Calamites.*

Photograph 7. Transverse section of Mr. WILD's specimen, at some distance from the base of the branch, showing typical Calamitean structure, with a large pith-cavity, and 24 bundles, each with its canal. C.N. 1941. × about 10.

Photograph 8. Another section of the same, nearer the base. Pith-cavity much smaller, bundles normal, but only 14 in number. C.N. 1934. × about 10.

Photograph 9. Third section of the same, taken close to the base. Pith of minute size, with small irregular cavity, probably of *post-mortem* origin. Only 10 bundles, very crowded together, and with no distinct canals. C.N. 1933A. × about 10.

Photographs 10–13. *Calamostachys Binneyana.*

Photograph 10. Part of a radial section through a large strobilus. There are 18 whorls of bracts in the specimen, of which 4 are shown. Between them are

the whorls of sporangiophores, of which 5 are shown, with their sporangia. Note the well-preserved central cylinder of the axis. C.N. 1022. × about 8.

Photograph 11. Part of a tangential section of the same specimen, showing the alternate whorls of coherent bracts, and of sporangiophores. In the former note the vascular bundles. The sporangiophores are seen in transverse section, each surrounded by its 4 sporangia. C.N. 1022A. × about 8. See also Plate 81, figs. 27 and 28.

Photograph 12. Transverse section passing through a whorl of coherent bracts, of which there are 13. Their vascular bundles can be seen. The small transverse sections, seen immediately outside the whorl, are those of bract-tips rising up from below. They alternate with the bracts of the next whorl. The still smaller transverse sections, seen in some places between the larger, are those of extreme tips of bracts from the second whorl below. C.N. 997. × about 20.

Photograph 13. Transverse section passing through a whorl of 6 peltate sporangiophores, some of which are shown completely, with the sporangium attached to the lower surface of the peltate expansion, at its edge. Here, again, the tips of the two whorls of bracts below are shown in transverse section surrounding the strobilus. C.N. 1020. × about 16.

PLATE 74.

Photograph 14. *C. Binneyana.* Transverse section of strobilus, passing through an internode. In the axis the stele has four prominent corners, with a bundle and its canal at each corner. A ring of sporangia surrounds the axis, and beyond these again are seen the extremities of bracts, some in section, others in surface-view. C.N. 1037A. × about 16.

Photograph 15. *Calamostachys Casheana.* Tangential section. Parts of three whorls are shown. All the sporangia are macrosporangia except one. The single microsporangium belongs to the middle whorl, and to a sporangiophore which also bears three macrosporangia. C.N. 1587. × about 18. See also Plate 82, fig. 38.

Photograph 16. Transverse section of the same specimen. Only macrosporangia are shown. The central cylinder has formed some secondary wood. C.N. 1588. × about 25. See also Plate 82, figs. 36 and 37.

Photograph 17. *Calamostachys sp.* Part of a radial section of the strobilus. The bracts and sporangiophores are obliquely ascending, not horizontal as in *C. Binneyana.* C.N. 1896. × about 8.

Photograph 18. Tangential section of the same specimen. C.N. 1897. × about 8.

PLATE 75.

Sphenophyllum plurifoliatum.

Photograph 19. Transverse section of a stem of moderate age, which has already cast off its primary cortex. The triarch primary xylem is shown; also the radially arranged fascicular and interfascicular secondary wood and, beyond that, the layers of phloëm and periderm. C.N. 894. × about 18. See also Plate 83, fig. 43.

Photograph 20. Transverse section of another stem at a similar stage. The details of the wood and of the periderm are especially clear. C.N. 899. × about 18.

Photograph 21. Transverse section of a very advanced stem. Structure of wood identical with that of previous specimens. To the exterior, successive scales of bark are shown. C.N. 1893. × about 8.

Photograph 22. Part of a transverse section of a still older stem, with secondary wood reaching 37 elements in thickness. Details of wood, especially xylem-parenchyma, very clear. Phloëm only partially preserved, but 4 successive layers of periderm are present. C.N. 901. × about 30.

PLATE 76.

Photograph 23. *Sphenophyllum insigne.* Transverse section of a stem, which still retains its primary cortex. Triarch primary wood has a canal at each angle. 5–8 layers of secondary wood, with narrow medullary rays, have been formed. There are traces of periderm within the primary cortex. C.N. 919. × about 30.

Photograph 24. *Sphenophyllum* from Autun. Transverse section of a specimen presented by M. RENAULT. Observe the *hexarch* primary xylem, which is imperfectly differentiated towards the centre. Secondary wood as in *S. plurifoliatum.* C.N. 929. × about 12.

Photograph 25. Part of an approximately transverse section through the strobilus of *S. Dawsoni.* The central cylinder is absent, but leaf-trace bundles, within the cortex, are well shown. Several sporangia show attachment to sporangiophore, with its vascular bundle. C.N. 1898, H. × about 14.

Photograph 26. Approximately transverse section of a small strobilus of the same. The triangular xylem is shown in the axis. Part of the whorl of bracts seen is surface view, and sections of other bracts more to the exterior. One sporangium is shown attached to sporangiophore. C.N. 1898, I. × about 12.

PLATES 77–85.—Figures from camera-lucida drawings executed by Mr. GEORGE BREBNER.

PLATE 77.

Calamites.

Fig. 1. Transverse section of a very young twig. The pith is nearly solid, but slightly disorganized near the centre. There are seven vascular bundles, each with its canal. In most of the canals rings can be seen (as at *px*), which are the remains of the primitive tracheæ. Secondary wood, both fascicular and interfascicular, has just begun to be formed. The simple cortex is well preserved. C.N. 116*. × 100.

Fig. 2. Transverse section of a larger twig, but at a still earlier stage of development. The pith is hollow. There are twelve bundles, each with a canal, on the outer edge of which is the primary xylem. No secondary tissue has yet appeared. The cortex shows little differentiation. This is another section of the same specimen which is shown in Plate 72, photograph 1. C.N. 1561. × 50.

Fig. 3. Part of a transverse section of a larger and more advanced stem, the same as that of which another section is shown in Plate 72, photograph 2. A broad outer zone of pith is preserved. Two vascular bundles are shown. About twelve layers of secondary wood have been formed. The narrower elements belong to the secondary medullary rays. Interfascicular wood is already formed across the principal rays. The phloëm and cambium are disorganized, but their position is evident (*ph*). The well-preserved cortex is differentiated into two distinct layers. C.N. 14. × 50.

Fig. 4. Oblique section of a young branch; its cortex was preserved, but is not shown. The pith is hollow. There are twelve vascular bundles. In the canal of each bundle the fragmentary rings and spirals of the primitive tracheæ, or protoxylem, are seen, as at *px*. They sometimes extend to the inner margin of the canal (see especially the bundle marked *a*). Only the primary xylem of the bundles exists at this stage. C.N. 1002. × 100.

Fig. 5. Part of a radial section passing through the primary wood of a bundle. On the left are pith-cells. In the middle is the canal; which is still partly filled by the disorganized remains of the protoxylem (*px*). The tracheæ are partly annular, partly spiral. Towards the right they become more continuous. Still further to the right we see the persistent scalariform tracheæ (*sc*) of the primary wood external to the canal. C.N. 20A. × 200.

Fig. 6. Part of a transverse section, showing a leaf-trace bundle passing out horizontally through the secondary wood. On the left are pith-cells; *px*, protoxylem of a bundle passing into the next internode. The reticulated tracheæ

belong to the nodal wood. The tracheæ of the foliar bundle, *f*, are spiral and scalariform. C.N. 118*. × 150.

PLATE 78.

Calamites.

Fig. 7. Part of a radial section, showing a leaf-trace bundle passing out through the nodal and secondary wood; disorganized pith (*p*) is on the left. The nodal wood can be distinguished by its short tracheæ. The leaf-trace consists of tracheæ (on some of which the spiral thickening is seen) and surrounding parenchyma. The section not being quite in the plane of the outgoing bundle, the latter appears to die out towards the right. *px*, protoxylem of bundle below the node. C.N. 22 × 100.

Fig. 8. Part of a tangential section, showing a leaf-trace bundle cut transversely. The section passes through the inner part of the secondary wood. The pitting is almost entirely confined to the radial walls of the tracheæ. The shaded parts of the latter represent the unpitted tangential walls; the parts left white are in section; several secondary rays are shown (as at *r*). Some of the tracheæ show traces of transverse septa, but most of these appearances are due to oblique section of their tangential walls. The leaf-trace has a gap, where some of its primitive tracheæ are disorganized. It is surrounded by parenchyma. C.N. 20B. × 100.

Fig. 9. *A*. Short tracheide and neighbouring cells, in tangential section, to show bordered pits. Towards the parenchyma the border is unilateral (as at *a*). C.N. 20A (same specimen as 20B, but from a section nearer the pith). × 200.

B. Wall between two tracheæ, to show bordered pits, in tangential section. C.N. 1554 (shown in Plate 72, photograph 6). × 500.

Fig. 10. Part of radial section, passing through a node. The pith is to the left. Above the node part of a primary ray (*r*) is shown. The canal of a bundle, containing remains of the protoxylem (*px*) passes up to the node from below. The protoxylem is continuous with the innermost elements of the nodal wood. The rest of the nodal wood is continuous with the persistent primary xylem (*x*) immediately outside the canal. C.N. 21. × 50.

Fig. 11. Tangential section, to show course of vascular bundles. Three outgoing leaf-trace bundles are shown, in transverse section, at the node. Only the alternate bundles pass out at this node; the intermediate bundles do not pass out, but fork and attach themselves to the neighbouring strands. The relatively broad, small-celled rays (as at *r*) show that the section passes near the pith. C.N. 26. × 13.

Fig. 12. Part of transverse section, showing cortex and outer layers of wood (*x*).

Remains of the phloëm (*ph.*) are seen. The cortex consists of two distinct layers (*c* and *c'*); the outer layer becomes more sclerenchymatous towards the periphery. C.N. 118*. × 50.

Fig. 13. Another part of the same section showing a phloëm-group (*ph*). The cambium (*cb*) between wood and phloëm is also preserved, and the phloëm itself is complete, though crushed. The large cells above belong to the cortex (*c*) C.N. 118*. × 150.

Fig. 14. From the same section, showing a small portion of wood (*x*), cambial cells (*cb*) and their derivatives, and cortex (*c*). C.N. 118*. × 150.

The figs. 12, 13, and 14 are from the section, a part of which is shown in Plate 72, Photograph 3.

PLATE 79.

Calamites.

Fig. 15. Tangential section passing through a principal medullary ray near the pith. On either side are seen tracheides and one or two secondary rays (as at *r*). The principal ray is entirely parenchymatous; the elements towards the middle are quite short; those near the edges are narrower and more elongated (*m*). C.N. 65. × 50.

Fig. 16. From another section of the same stem, showing a principal ray further towards the exterior. The whole ray is narrower; the marginal cells (*m*) are more elongated, and are already partly replaced by tracheides. The ray to the left (*r*) may probably have been cut off from the principal ray by interpolated tracheides. C.N. 66. × 50.

Fig. 17. A third section of the same stem, still further towards the exterior. The principal ray is no longer continuous, but is completely broken up by interpolated tracheides. Some of its isolated parts (*r*) are quite similar to secondary rays. C.N. 67. × 50.

Fig. 18. Part of a transverse section showing cortex, and a small part of the secondary wood (*x*); the gap between them was caused by the growth of a Stigmarian rootlet, which is not figured. Remains of the phloëm (*ph*, are shown. Many of the cortical cells, especially those at a short distance from the interior, show recent tangential divisions, indicating the formation of periderm (*pd*). From a slide (No. 6) prepared by Mr. LOMAX, in the possession of D. H. SCOTT. × 70.

Fig. 19. Part of a median section, passing through a diaphragm. The cells towards both surfaces of the diaphragm have undergone regular tangential divisions (best shown on the upper surface), forming a layer of periderm. C.N. 132***. × 30.

Fig. 20. Part of a transverse section passing tangentially through the base of a branch,

which is inserted between two bundles (*v.b.*) of the main stem. The primary vascular bundles (*v.b′.*), and interfascicular tissue of the branch are shown, and the connections with the wood of the main stem. C.N. 132** (from same stem as the last). × 30.

PLATE 80.

Figs. 21 and 22. *Calamites.*

Fig. 21. Part of a tangential section, passing through the primary wood, and showing the base of a branch. Near the bottom of the figure the section has touched on the canals of two bundles, and shows their disorganized protoxylem (*px.*). All the tracheæ have tangential pits—characteristic of the inner wood. In the direction of the arrow (*f*), a foliar bundle is shown. In the same straight line, further to the right, is another group of cells, which represents a similar bundle at the point when it begins to curve outwards. The branch has a minute pith, surrounded by groups of primary xylem. The connection of the latter with the nodal wood of the stem can be clearly seen at the lower side of the branch Secondary wood has only been formed towards the upper side of the branch. The connection with the wood of the stem is entirely from below. From a slide (No. 53) prepared by Mr. LOMAX, in the possession of D. H. SCOTT. × 30.

Fig. 22. *A.* Part of a transverse section of a very large stem, showing in median section, the base of an occluded branch. The pith of the main stem is below the figure. In the branch the pith tapers towards the base. The connection of the wood of branch and stem is shown. Midway between the inner and outer limits of the wood of the stem, at the level indicated by the arrows, the pith of the branch comes to a sudden end, and is replaced by secondary wood seen in transverse section. × 6.

B. Portion of same enlarged, showing transition from pith of branch (*p*) to anomalous wood (*x*) in region indicated by the arrows in *A.* × 70. C.N. 134*.

Figs. 23–26. *Calamostachys Binneyana.*

Fig. 23. From a transverse section of a strobilus, showing the central cylinder or stele of the axis. The section passed through a fertile node, bearing 7 sporangiophores. The stele is obtusely triquetrous, with the vascular bundles at its prominent corners. There appear to have been 7 bundles in all; the projecting points of the xylem (*sp*) mark the places where the bundles passing out to the sporangiophores were given off. One such bundle is partly preserved (sp^+). On the inner side of the bundles in the cylinder are

irregular canals, in which remains of the protoxylem (*px*) can be traced. All the tissue within the ring of bundles is pith. A few tangential interfascicular cell-divisions have taken place. C.N. 991. × 70.

Fig. 24. From a transverse section of another strobilus, showing the stele and part of the cortex. Here there are probably 6 bundles, in groups of 2 (as at *px*, where their protoxylem is shown). Secondary thickening has made considerable progress. In other respects the structure is similar to that in the last figure. C.N. 1016. × 70.

Fig. 25. From a transverse section of a strobilus, showing the quadrangular stele and part of the cortex. There are 4 vascular bundles, one at each corner. Tangential divisions have begun in the cells of the interfascicular tissue. *px*, the 4 groups of protoxylem. C.N. 1013A. × 70. Compare Plate 74, photograph 14.

Fig. 26. Part of a somewhat oblique transverse section, showing a vascular bundle in connection with the cortical tissues. *p,p*, pith; *x,x*, xylem; *px*, protoxylem; *ph*, phloëm-group; *pc, pc*, probable pericycle; *c,c*, cortex. C.N. 1013. × 200.

PLATE 81.

Calamostachys Binneyana.

Fig. 27. Part of an approximately median longitudinal section of the axis of a large strobilus. *p,p*, the wide pith of the cylinder; on either side is the xylem of a vascular bundle. Two canals are shown with remains of the protoxylem (*px*), (*px*). *c,c*, the cortex, of which only the inner layers are shown. The section passes through a whorl of sporangiophores. C.N. 1022A. × 70.

Fig. 28. Tangential section through a vascular bundle of the same strobilus. The section passes through a node bearing a whorl of bracts (the second sterile node from below, shown in photograph 10, on Plate 73). The canal of the bundle, with the protoxylem (*px*), is shown both above and below the node. The nodal wood has short reticulated tracheides. In the internode the tracheæ are generally scalariform. The parenchyma on either side belongs to the stele. C.N. 1022. × 70.

Figs. 27 and 28 are from the same preparations as photographs 10 and 11, on Plate 73. Fig. 27 is from a part not shown in the photographs.

Fig. 29. Peltate sporangiophore, with a sporangium attached, from an approximately transverse section of a strobilus. The vascular bundle is shown in the axis of the sporangiophore, and a branch-bundle is seen passing through the peltate expansion, to the base of the sporangium. The sporangium is attached to the edge of the peltate scale, at *a*. Within the sporangium are numerous spore-tetrads, enclosed in their mother-cell membranes. C.N. 996. × 70.

Fig. 30. Part of a tangential section of a strobilus, showing a sporangiophore-pedicel (*sp*) in transverse section, surrounded by its 4 sporangia. The vascular bundle of the sporangiophore is seen. Parts of the adjacent whorls of coherent bracts, *br*, *br*, are shown. Three vascular bundles are shown in the lower, and two in the upper whorl. C.N. 1023. × 50.

Fig. 31. Details of sporangium-wall,

A. In surface view; "buttresses" seen (as at *bu*) projecting from cell-walls into interior of cells;

B. In transverse section of sporangium (tangential of strobilus). Here the "buttresses" (*bu*) are seen from the side, with the thin cell-wall between them. Such a section cuts *across* the cells shown in A.

C. In longitudinal section of sporangium (transverse or radial of strobilus). Here the narrow edges of the "buttresses" (*bu*) are shown. Such a section cuts the cells shown in *A lengthwise.* The difference in the thickness of the wall in *B* and *C* is accidental. C.N. 1003. × 200.

Fig. 32. Part of a tangential section, passing through the peltate expansions of the sporangiophores (*sp*), 4 of which are shown, and also part of the whorl of bracts (*br*) between them. In *sp.* 1 the right-hand dichotomy of the vascular bundle (*vb*) is well shown. In *sp.* 2 the section shows one bundle in transverse section, and a branch-bundle cut longitudinally. In *sp.* 3 parts of the vascular bundles are shown. At two points the section passes through the concavities of the under surface of the scale, and shows part of the wall of 2 sporangia, *w.*, *w.*; *br′.*, *br′.*, outline of adjacent bracts. C.N. 1898A. × 30.

Fig. 33. Part of a sporangium containing spore-tetrads. The extremely unequal size of the different spores of the same tetrad is the point specially illustrated. In many cases (as at *b*) certain spores appear to be quite abortive. At *a*, a mature spore is shown, with the 3 radiating fissures in its membrane. C.N. 1007. × 100.

PLATE 82.

Figs. 34 and 35. *Calamostachys Binneyana.*

Fig. 34. Part of a sporangium containing spore-tetrads, to show abortive spores with normal sister-cells. In a tetrad towards the left-hand, 3 out of the 4 spores are abortive (*b*). C.N. 1011. × 100.

A, B, C, and *D.* Tetrads and spores more highly magnified.

A. A normal tetrad. All 4 spores are about equally developed. C.N. 1005. × 200.

B. A tetrad in which one spore is abortive. C.N. 1013A. × 200.

C. A tetrad with one abortive spore, and one of intermediate size. C.N. 1011. × 200.

D. Two mature spores to show fissures and thickening of the spore-membrane. C.N. 1007. × 200.

Fig. 35. Part of a sporangium, to show layer of parenchyma lining the sporangial wall. Within this are mature spores. C.N. 1008. × 150.

Figs. 36–39. *Calamostachys Casheana.*

Fig. 36. Transverse section of the axis of the strobilus. In the middle is the central cylinder, with a large pith, surrounded by 6 vascular bundles. The structure is the same as in fig. 24 (Plate 80), from *C. Binneyana* (*px.*, two of the proto-xylem-groups). There is a well-marked zone of radially arranged secondary xylem. Outside this are remains of thin-walled cells, and surrounding the whole is the well-preserved outer cortex. The outlines to the exterior mark the position of the sporangia. This is from the same preparation as photograph 16, on Plate 74. C.N. 1588. × 70.

Fig. 37. Section of a macrosporangium (that marked × in fig. 36), containing several macrospores (as at *ma*), and a large number of abortive spores (as at *b*). There are slight remains of tissue lining the sporangial wall. C.N. 1588.

A. Microspores from the tangential section of the same specimen. C.N. 1587.

B. Macrospores and abortive spores. C.N. 1587.

C. ,, ,, ,, C.N. 1588.

All the above × 100.

Fig. 38. Group of four sporangia from a tangential section, with the pedicel of their sporangiophore (*sp.*) between them. One is a microsporangium; the other three are macrosporangia. Among the macrospores abortive spores are seen. Also shown in Plate 74, photograph 15. C.N. 1587. × 30.

Fig. 39. Parts of two adjacent sporangia from a tangential section of the other specimen of this species. To the right is a microsporangium, containing microspores (*mi*) only. To the left is a macrosporangium, in which one of the macrospores (*ma*) and several abortive spores (*b*) are shown. C.N. 1025. × 100.

PLATE 83.

Figs. 40–44A. *Sphenophyllum plurifoliatum.*

Fig. 40. Obliquely transverse section of a moderately young stem. In the middle is the triarch primary xylem. The three protoxylem groups at the angles (*px.*), with their small, spiral or reticulated tracheæ, are clearly seen. The more central primary tracheæ are pitted. About four layers of secondary wood

have been formed. The parenchymatous cells at the corners of the tracheæ are shown. The wood is surrounded by secondary cortical tissues, probably including both phloëm and periderm. At *c*, *c*, remains of the primary cortex are present, but only a part of this has been drawn. C.N. 897. × 30.

Fig. 41. Part of an oblique section, showing a portion of the primary xylem. In the direction of the arrow (*px*) is a group of protoxylem, with spiral tracheæ, partly uncoiled. Adjoining these below are scalariform tracheæ, and below these again are pitted elements. Above the protoxylem a small portion of the secondary wood is indicated. C.N. 893. × 200.

Fig. 42. Part of an approximately transverse section, to show secondary wood, x^2; cambium, *cb*; and phloëm, *ph*. C.N. 882. × 70.

Fig. 43. Part of a transverse section (the same as that shown in photograph 19 on Plate 75); *x*, part of primary xylem; x^2, secondary xylem; *cb*, cambium; *ph*, phloëm; *pd*, internal periderm. C.N. 894. × 50.

Fig. 44. Part of a radial section through the secondary wood, showing the *radially-elongated* parenchymatous cells (as at *r*), passing between the tracheæ. C.N. 884. × 50.

Fig. 44A. Part of another, approximately radial section, showing the longitudinal strands of xylem-parenchyma, *x.p.*, *x.p.*, and portions of the radial cells connecting them. C.N. 903. × 50.

Figs. 45 and 46. *Sphenophyllum insigne.*

Fig. 45. Approximately transverse section of a young stem, without any secondary thickening. In the middle is the triarch primary xylem, with protoxylem at the three angles. Surrounding this are the primary cortical tissues. C.N. 911. × 50.

Fig. 46. Transverse section of a very young stem, showing part of a whorl of coherent leaves, in which two foliar vascular bundles are seen (*v.b.*). The fragments of tissue seen to the exterior are probably portions of leaves. *st* = stele of stem. C.N. 917. × 50.

PLATE 84.

Sphenophyllum insigne.

Fig. 47. *A.* Longitudinal median section, passing through a node. *l*, *l*, bases of leaves. × 13.

B. Portion of wood from the same preparation, seen in tangential, but somewhat oblique section. The scalariform markings of the tracheæ, and the medullary rays (*r*) are seen. *Cf.* fig. 50. C.N. 1420. × 100.

Fig. 48. Part of the transverse section of the largest stem, showing secondary wood, x^2; cambium, *cb*; phloëm, *ph*; and internal periderm, *pd*. C.N. 914. × 50.

Fig. 49. Part of the secondary wood of the same specimen, in radial section; *r*, medullary rays. C.N. 924. × 100.

Fig. 50. Part of the secondary wood of a large stem, in tangential section, showing the medullary rays (*r*), of various heights, and the scalariform pits of the tracheæ; compare with fig. 47B. C.N. 921. × 100.

Fig. 51. Part of a transverse section of the largest stem. x^2, secondary wood; *cb*, cambium; *ph*, phloëm; *pd*, inner layers of periderm. C.N. 913. × 100.

Fig. 52. Corresponding radial section from the same specimen; lettering as before. Note the elements in the phloëm resembling sieve-tubes.

The separation between periderm and phloëm is accidental; in other parts of the section they are continuous. The delicate layer which is severed is probably phellogen. C.N. 924. × 100.

PLATE 85.

Fig. 53. *Sphenophyllum insigne.* Part of a longitudinal section of the wood, passing through the canal, and showing the spiral tracheæ of the protoxylem, *px*. To the left of the canal is primary xylem, *x*; to the right the secondary wood, x^2, begins. The section is somewhat oblique.

From a stem of moderate size, with secondary wood 7–9 cells thick. C.N. 922. × 100.

Figs. 54–58. *Sphenophyllum Dawsoni.*

Fig. 54. Part of a longitudinal section of a small strobilus, showing 4 whorls of bracts. The section is partly radial, partly tangential. *x*, part of xylem of axis; *sp*, various sporangiophores, showing attachment to bracts. Fragments of sporangia, and numerous spores, are shown. C.N. 1898K. × 15.

Fig. 55. Part of a transverse section, through the whorl of bracts close to its insertion on the axis. From the section figured by WILLIAMSON, "Organization," Part XVIII., Plate 27, fig. 9. Three bundles are shown just separating from one another. *b.*, bundle going to a bract; *sp*, *sp*, bundles going to two sporangiophores. C.N. 1049A. × 200.

Fig. 56. Corresponding section from the same specimen, taken through the whorl of bracts, a little higher up than the last. From the section figured by WILLIAMSON, *loc. cit.*, Part XVIII., Plate 26, fig. 2. The three bundles have now quite separated, and the projecting bases of the sporangiophores are seen. *b*, bundle going to bract; *sp*, *sp*, bases of sporangiophores. C.N. 1049B. × 100.

Fig. 57. Transverse section through a sporangium, *sm*, and its sporangiophore, *sp*. In the former, delicate tissue lining the wall is shown, and within this the spores. In the sporangiophore, the xylem of the vascular bundle is evident. C.N. 1898H. × 60.

Fig. 58. Corresponding longitudinal section of a sporangium and part of its sporangiophore, showing the attachment. The vascular bundle of the sporangiophore is shown. The section is somewhat oblique. C.N. 1898E. × 60.

PLATE 86.

This contains figures, from photographs, of medullary casts of *Calamites*. For description, see text, pp. 896–899.

All the figures are much reduced. F is rather more than a quarter of natural size; all the rest are rather more than half natural size.

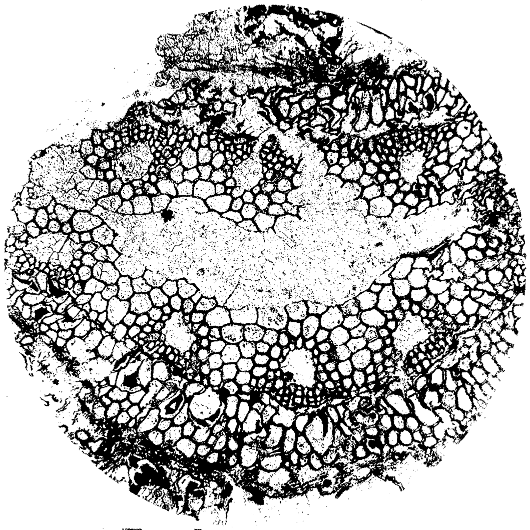


Fig. 1.

Fig. 2.

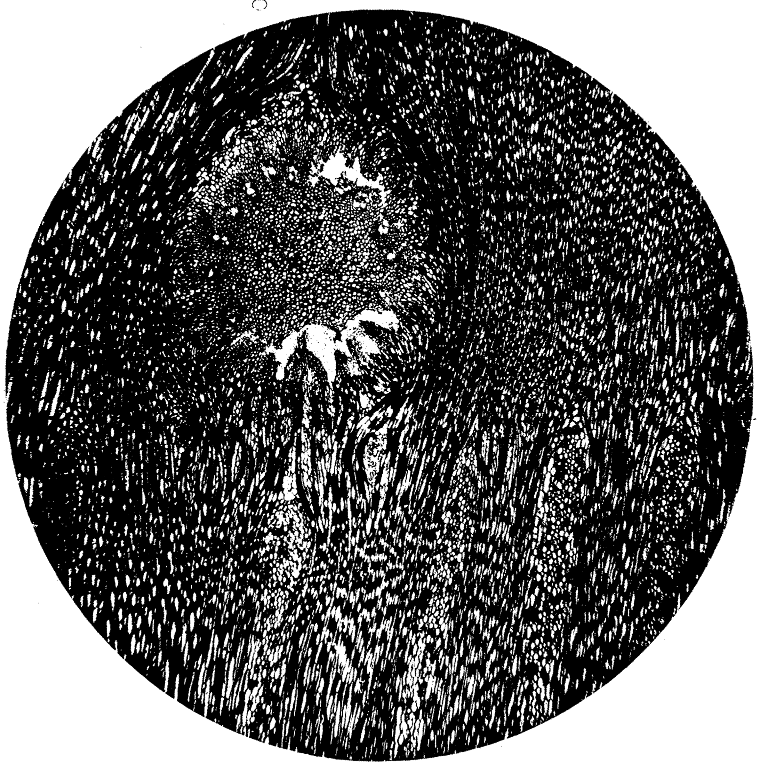


Fig. 6.

Fig. 3.

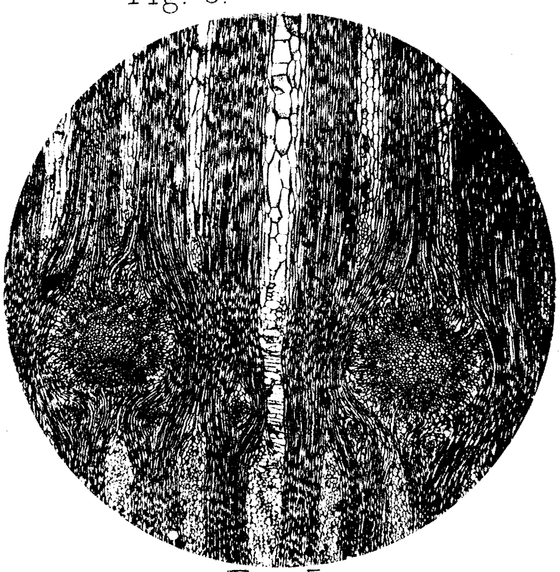


Fig. 5.

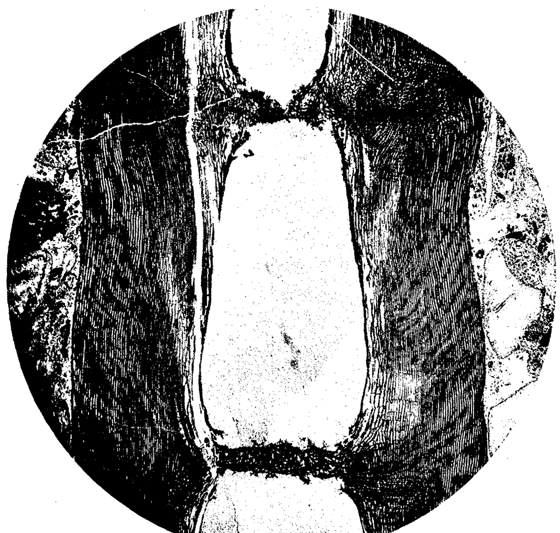


Fig. 4.

Figs. 1–6, Calamites.

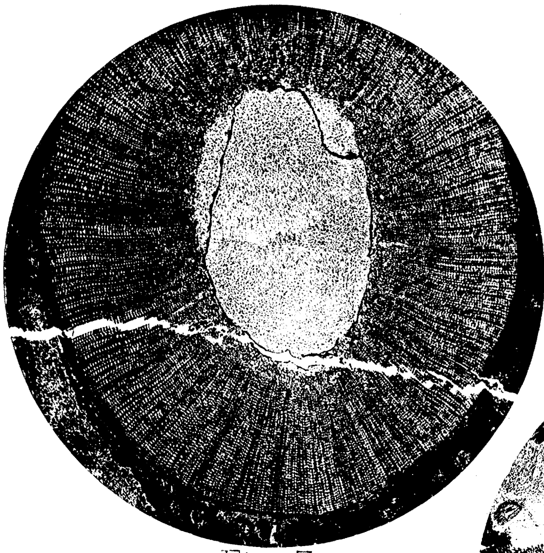


Fig. 7.

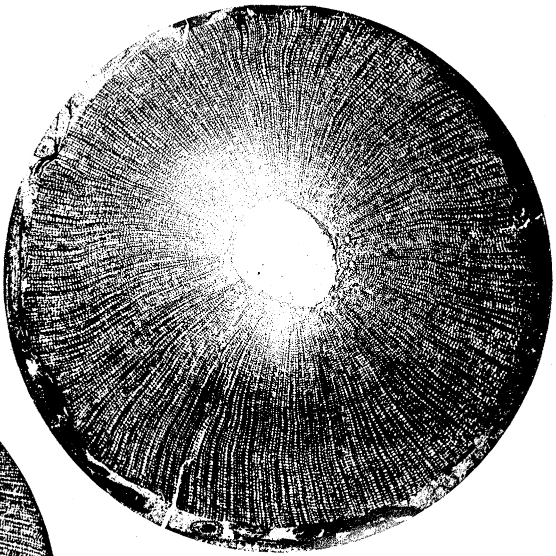


Fig. 8.

Fig. 9.

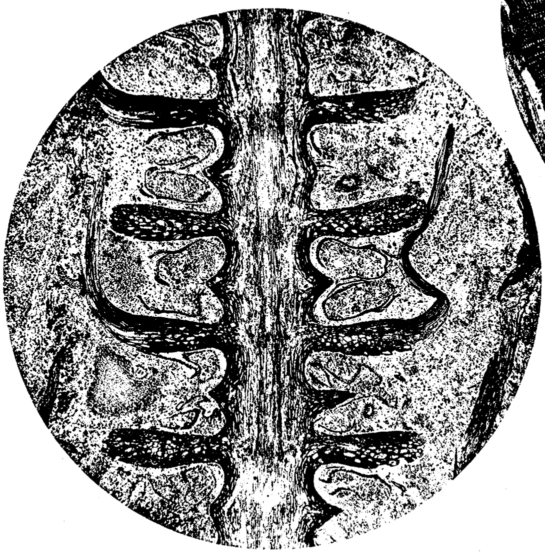


Fig. 10.

Fig. 11.

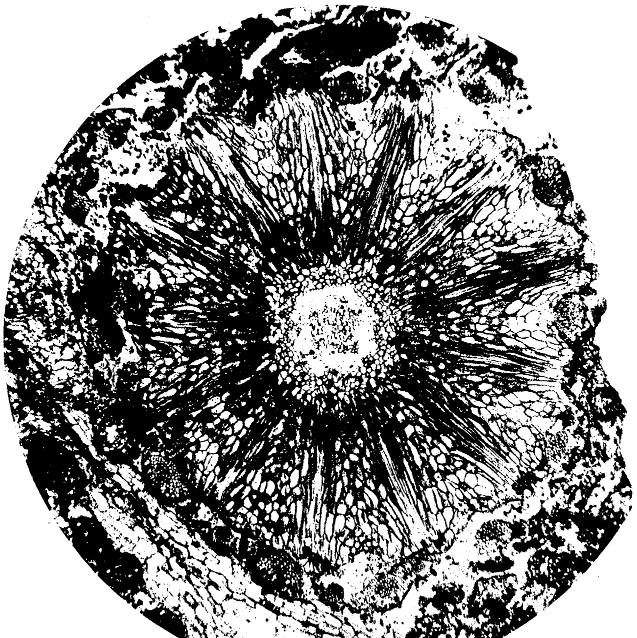


Fig. 12.

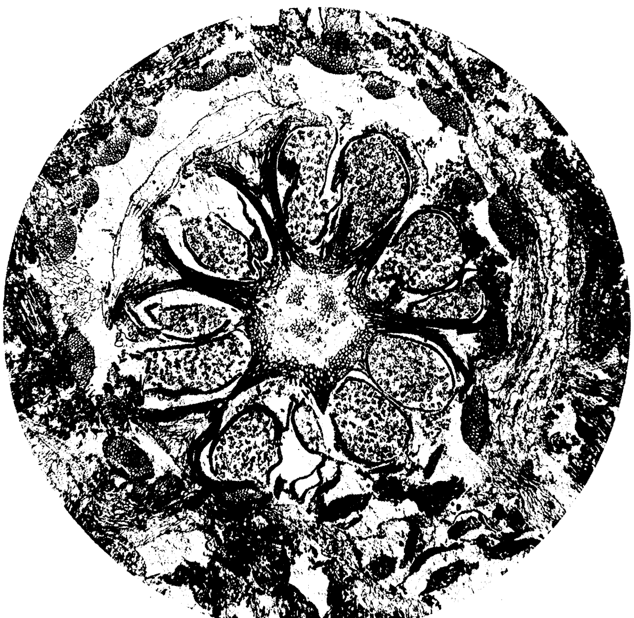


Fig. 13.

Figs. 7—9. Calamites.

Figs. 10—13. Calamostachys Binneyana.

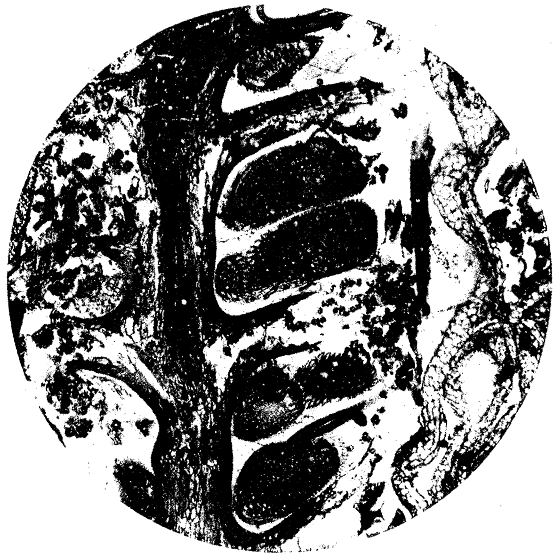


Fig. 17.

Fig. 14.

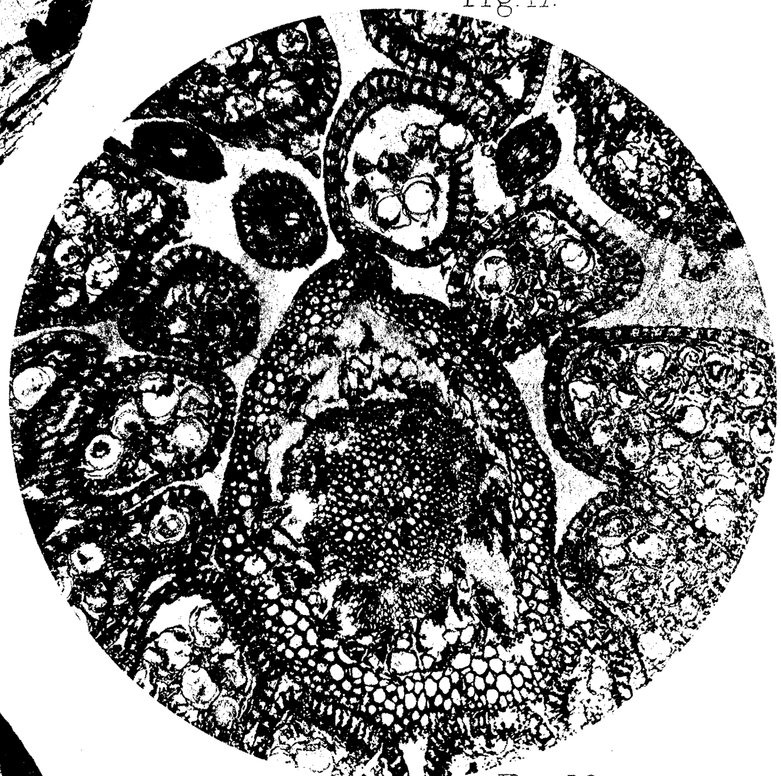


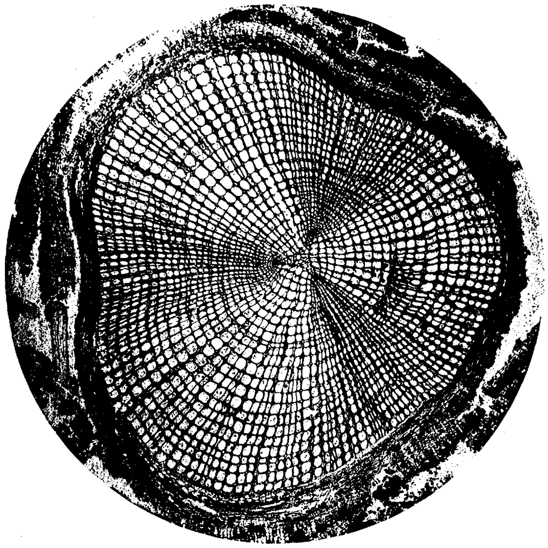
Fig. 16.

Fig. 15.

Fig. 18.

Fig. 14, Calamostachys Binneyana.
Figs. 15–16, C. Casheana. Figs. 17–18, Calamostachys sp.

Fig. 19.



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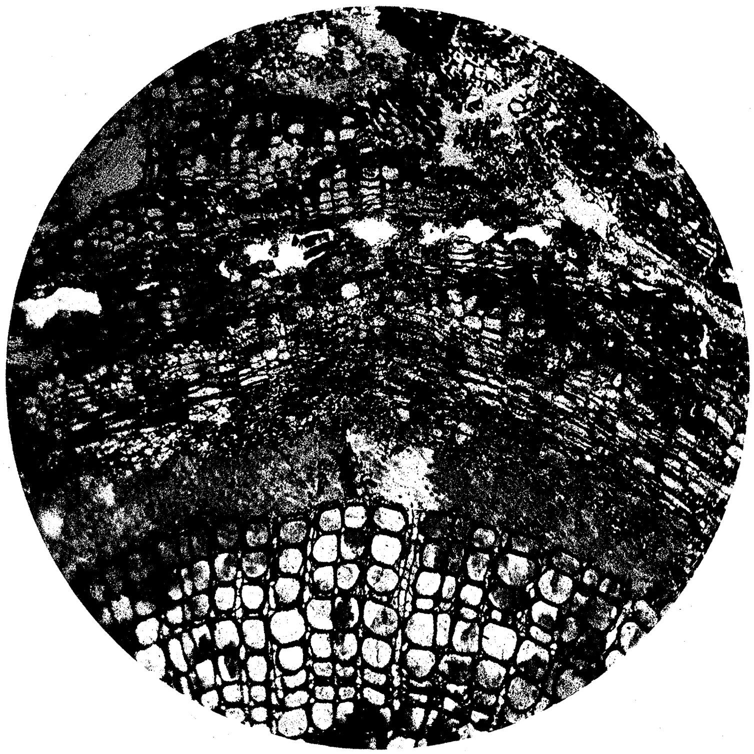


Fig. 22.

Fig. 20.

Figs. 19.—22. Sphenophyllum plurifoliatum.

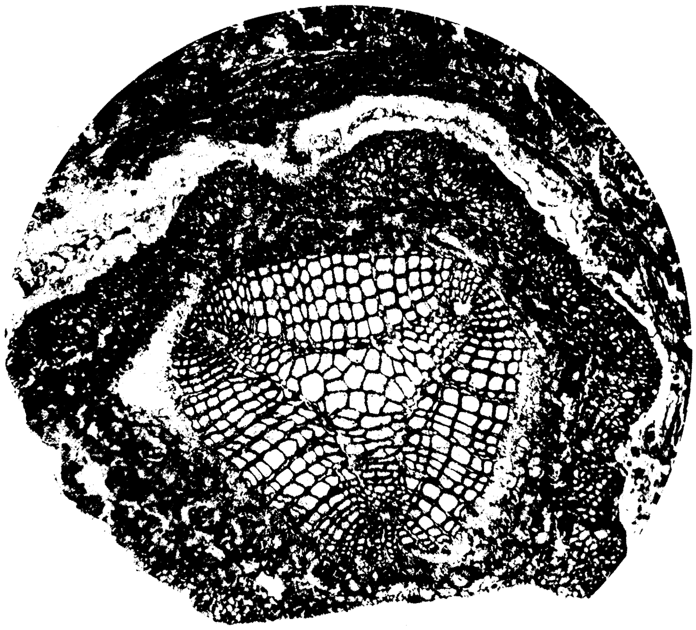


Fig. 23.

Fig. 24.

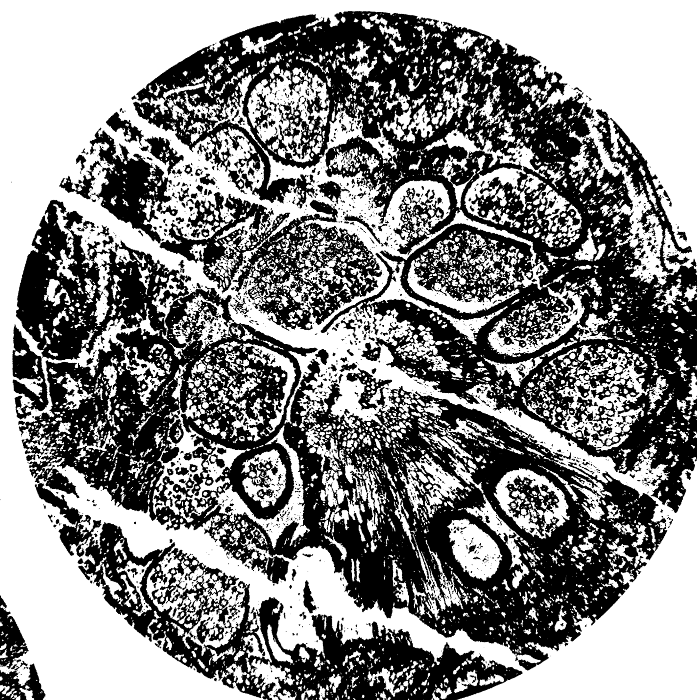
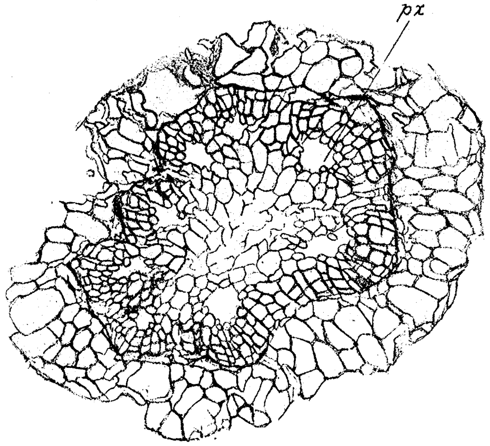


Fig. 26

Fig. 25.

Fig. 23, Sphenophyllum insigne. Fig 24, Sphenophyllum sp.
Figs. 25-26 Sphenophyllum Dawsoni.



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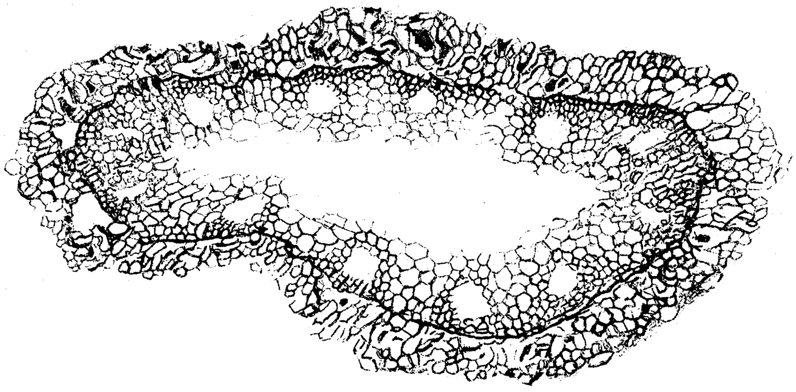

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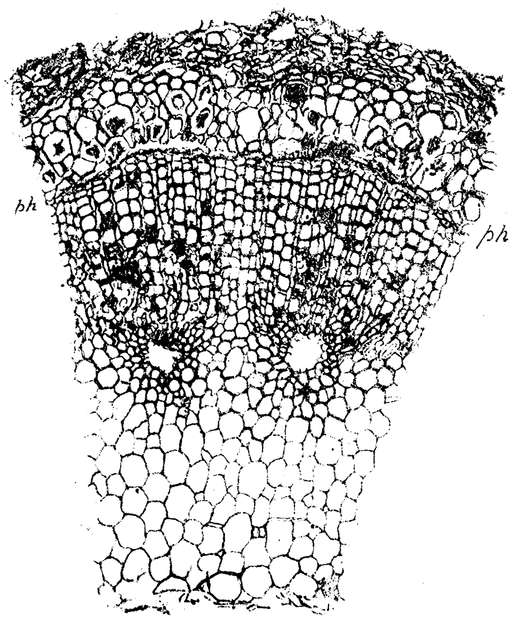

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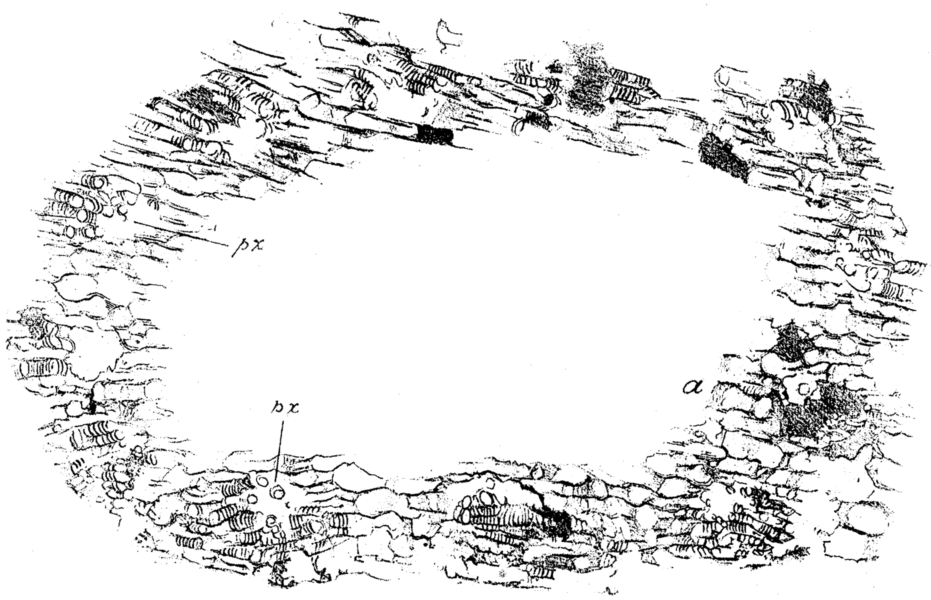


Fig. 4.

Fig. 5.

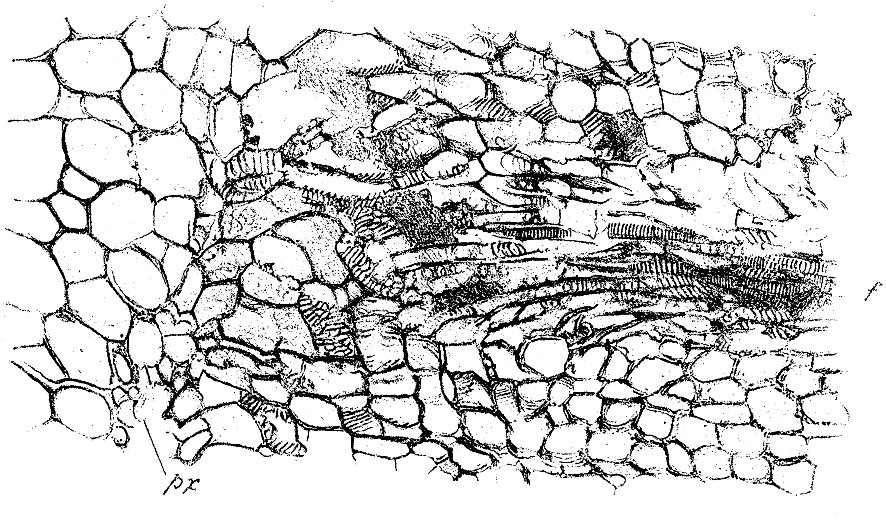
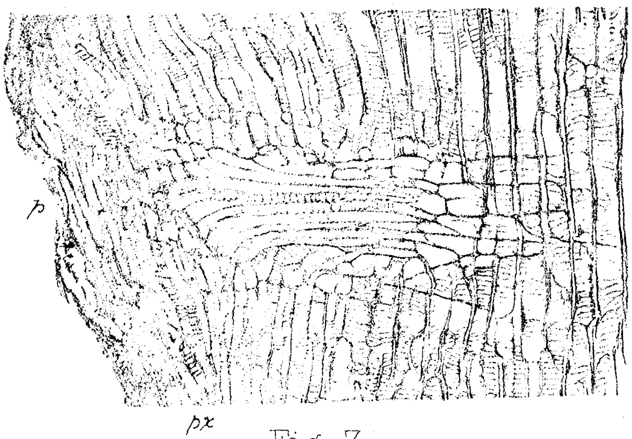


Fig. 6.

G. Brebner del.

Figs. 1–6, Calamites.



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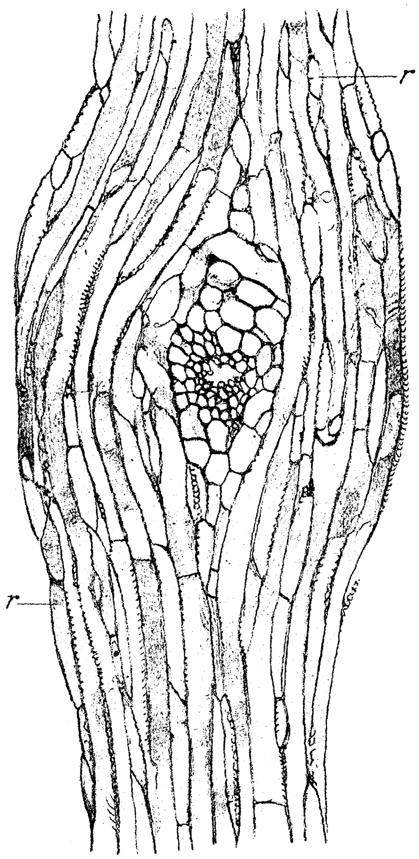

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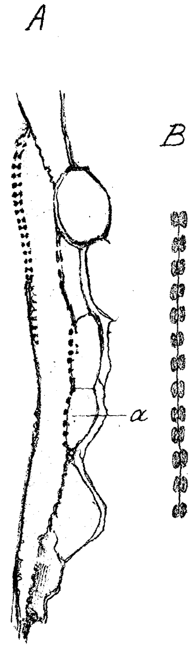

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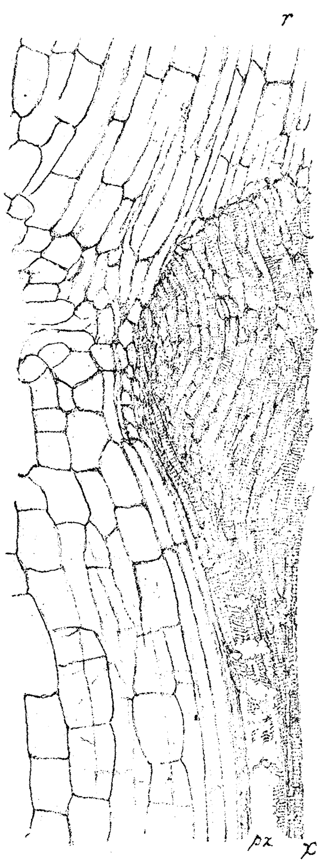

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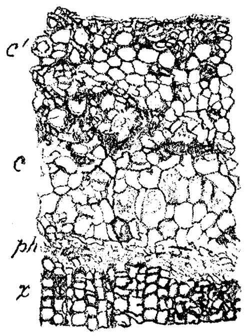

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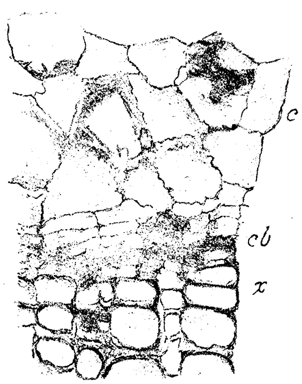

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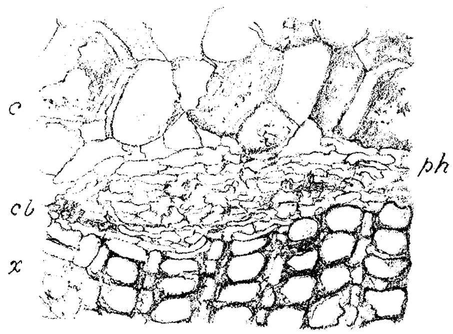

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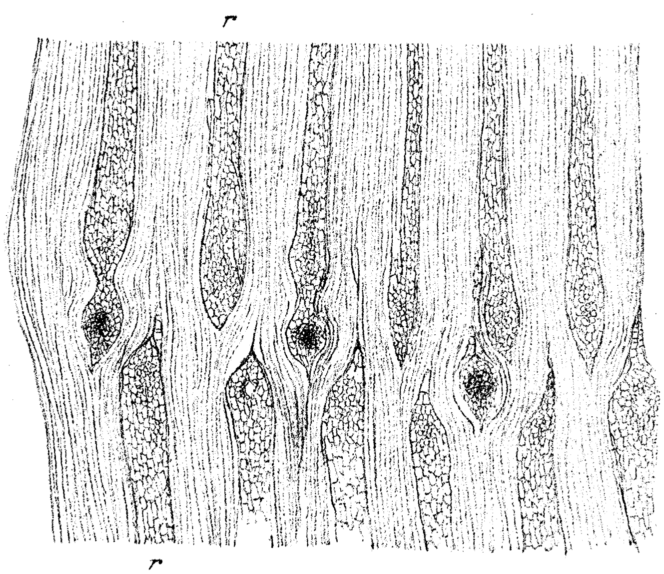

Fig. 11.

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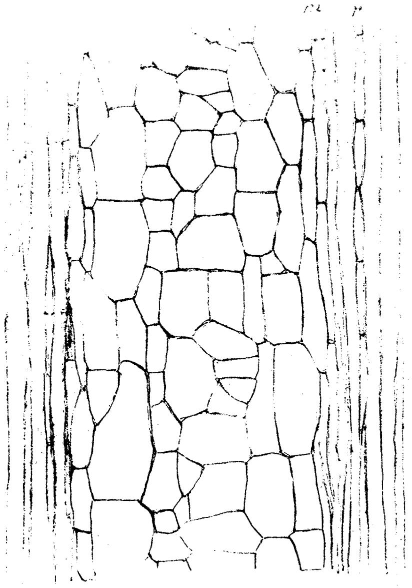
Figs. 7–14, Calamites.



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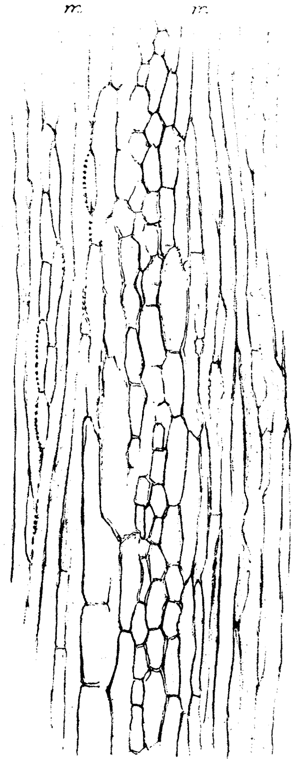

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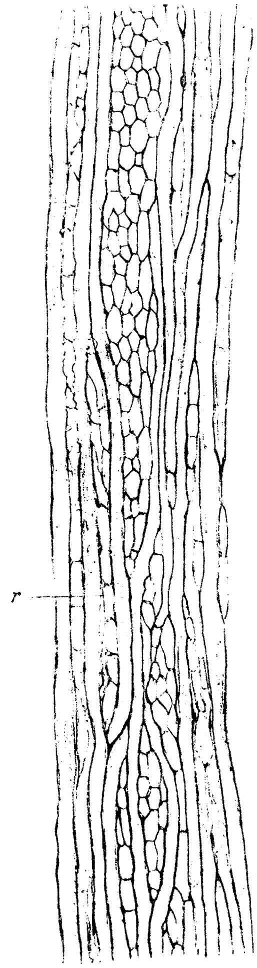

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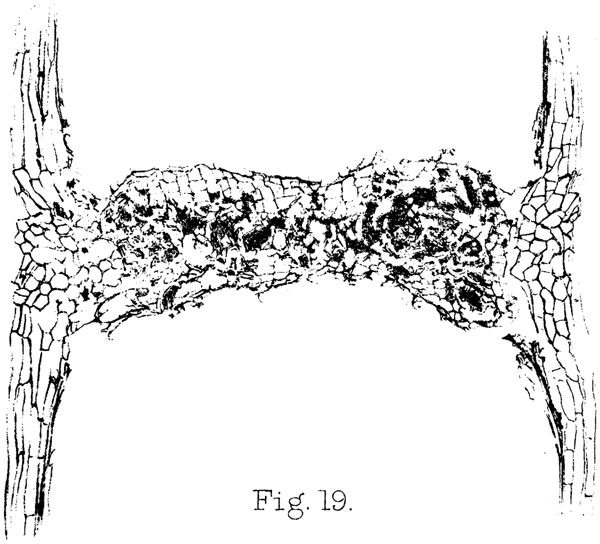
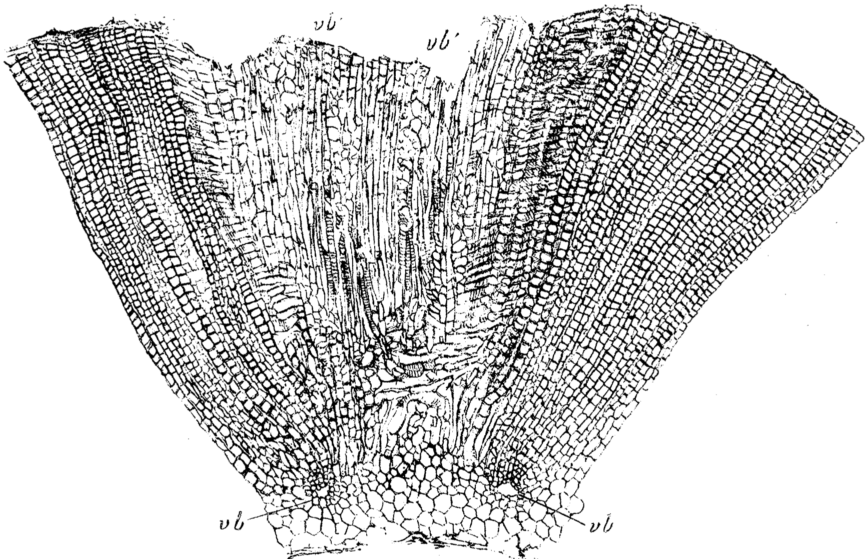


Fig. 19.

Fig. 18.



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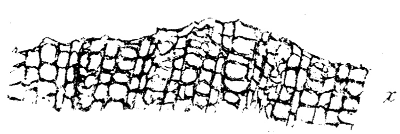

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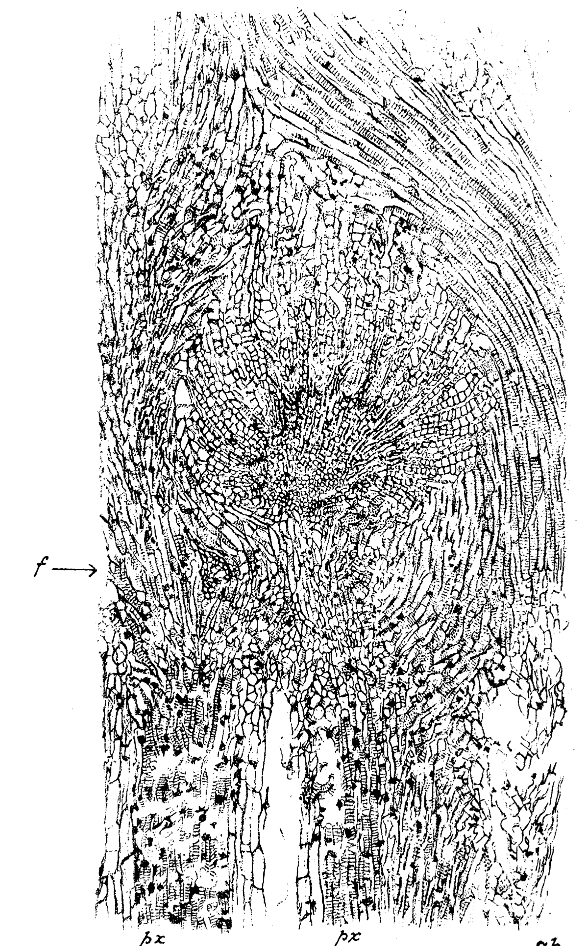
Figs. 15—20, Calamites.



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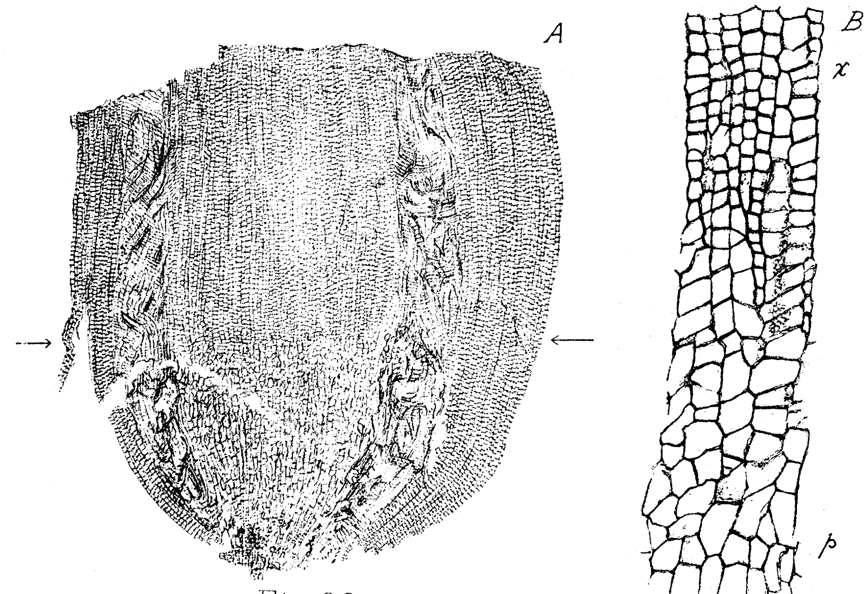

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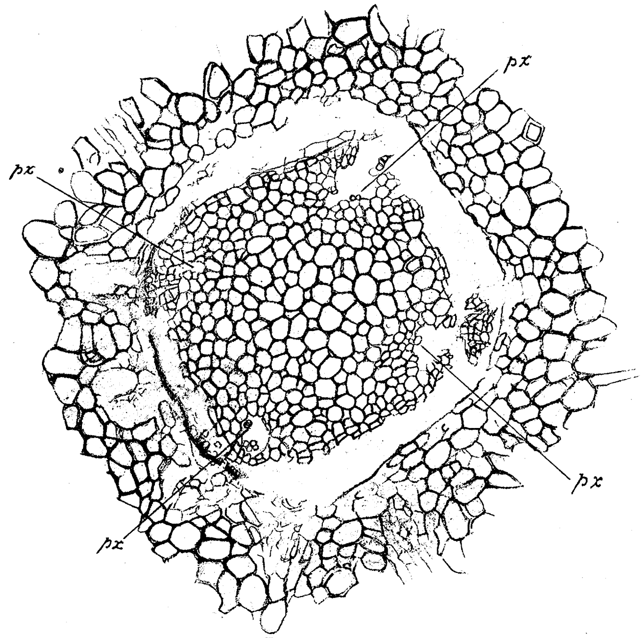

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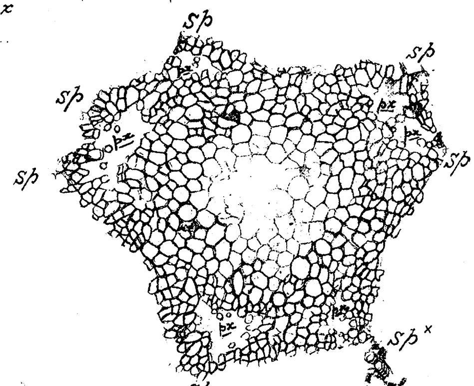

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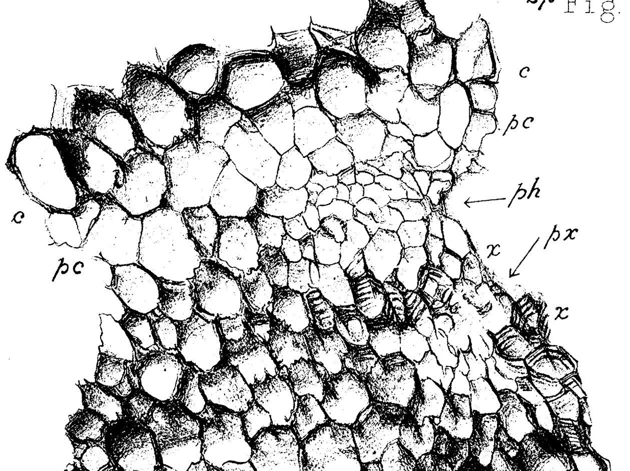

Fig. 26.

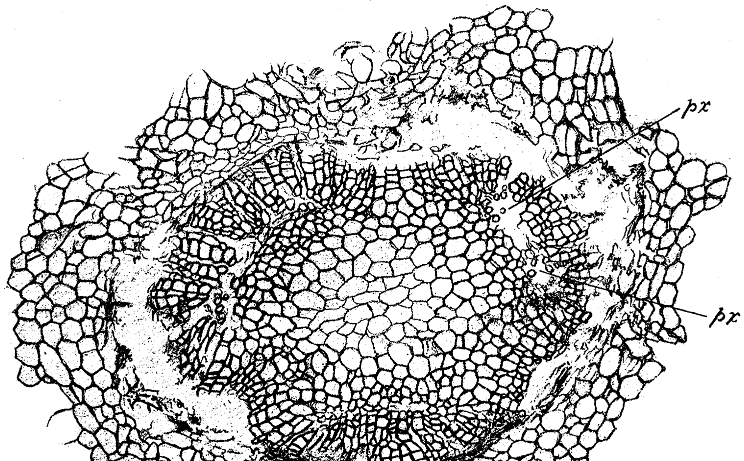

Fig. 24.

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Figs. 21, 22, Calamites.
Figs. 23—26, Calamostachys Binneyana.

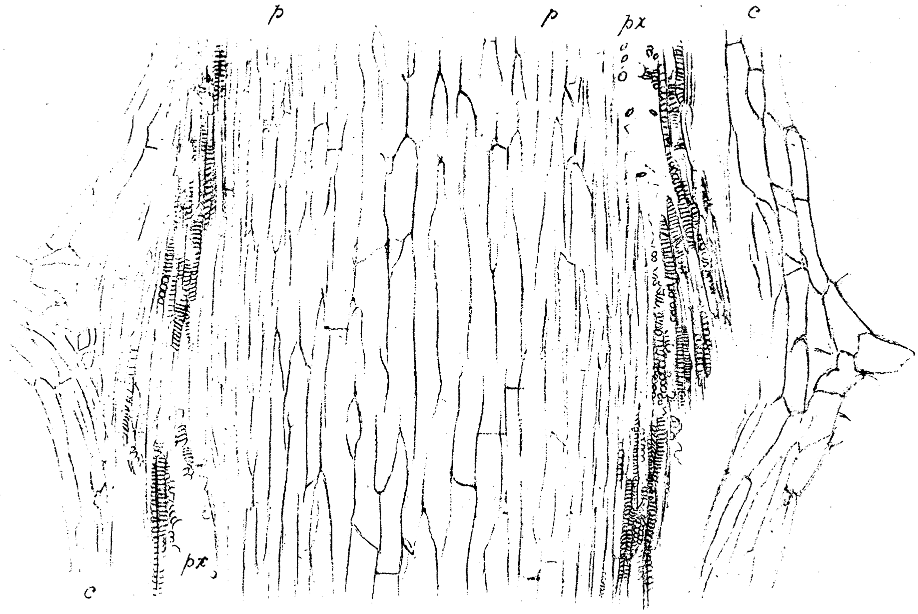


Fig. 27.

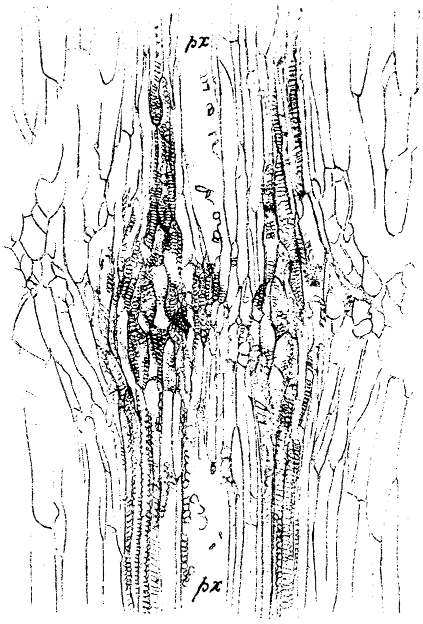


Fig. 28.

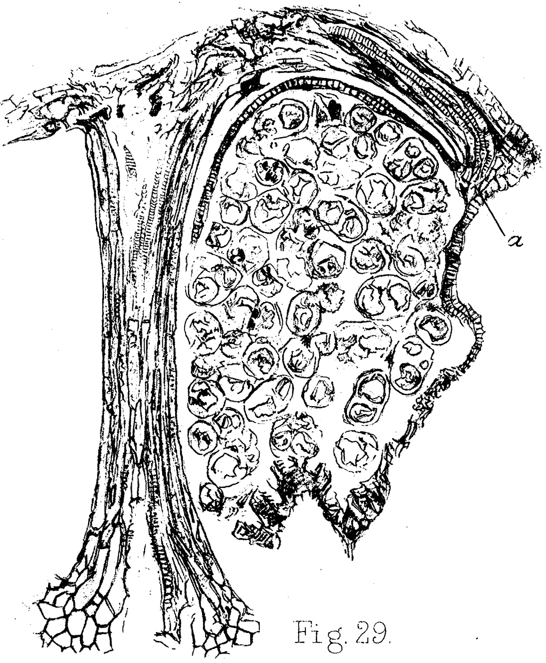


Fig. 29.

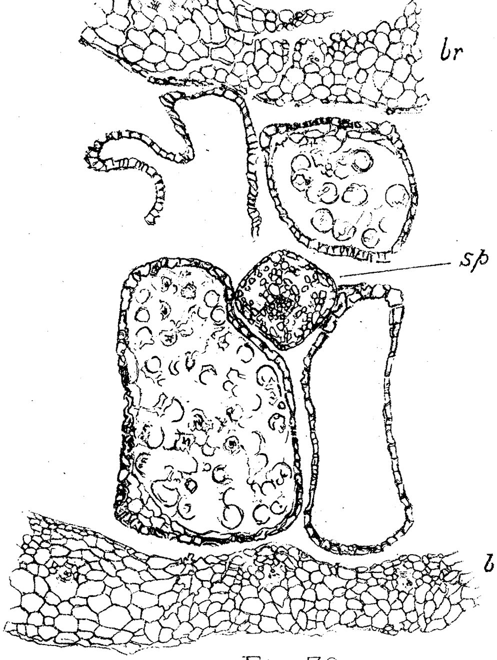


Fig. 30.

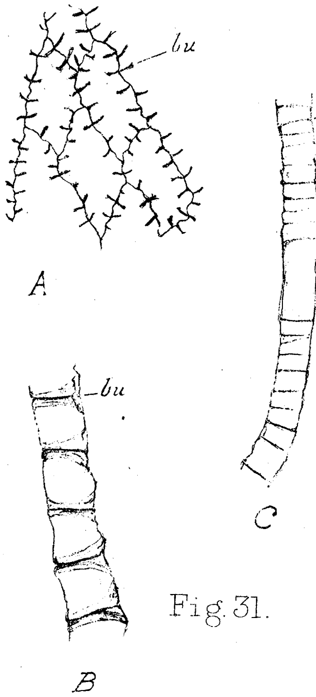


Fig. 31.

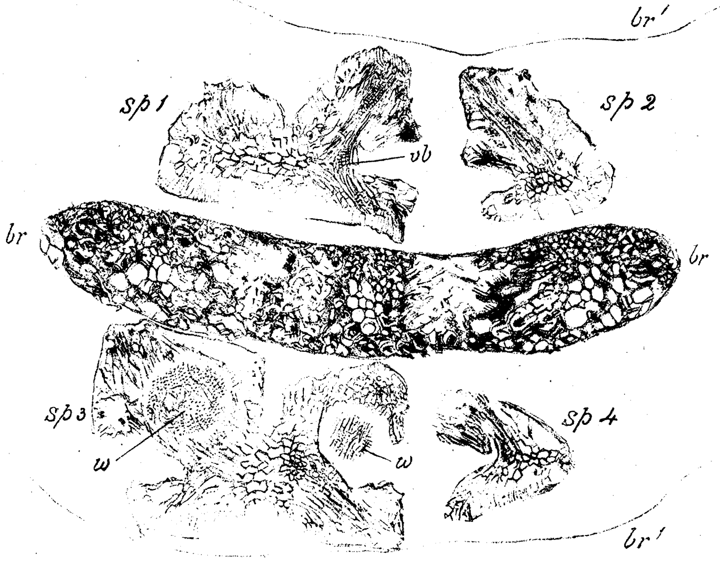


Fig. 32.

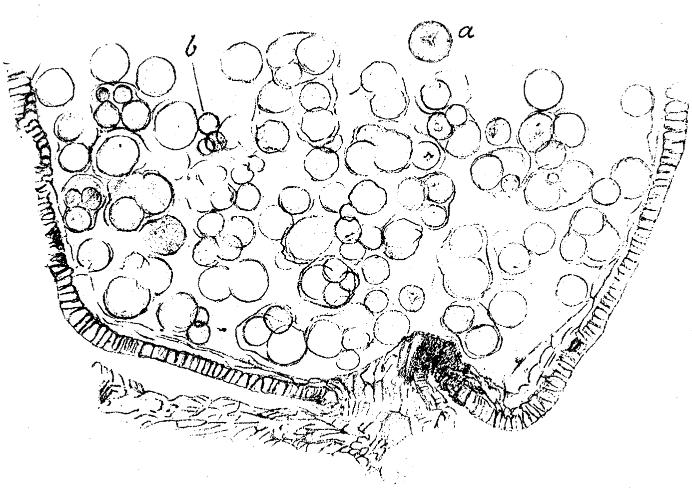
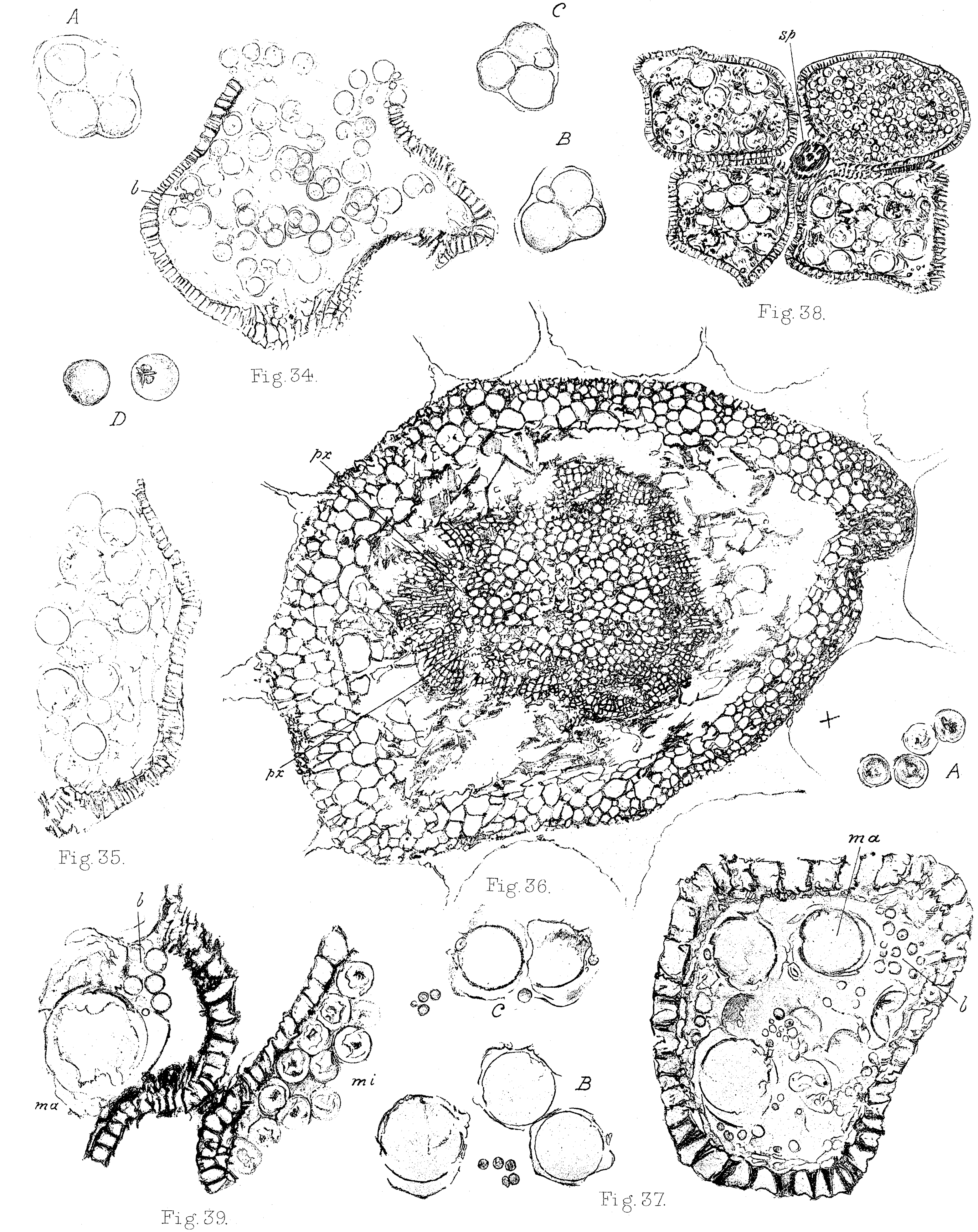


Fig. 33.

G. Brebner del.

Figs. 27–33, Calamostachys Binneyana.



G. Brebner del.

Figs. 34, 35, Calamostachys Binneyana.
Figs. 36-39, C. Casheana.

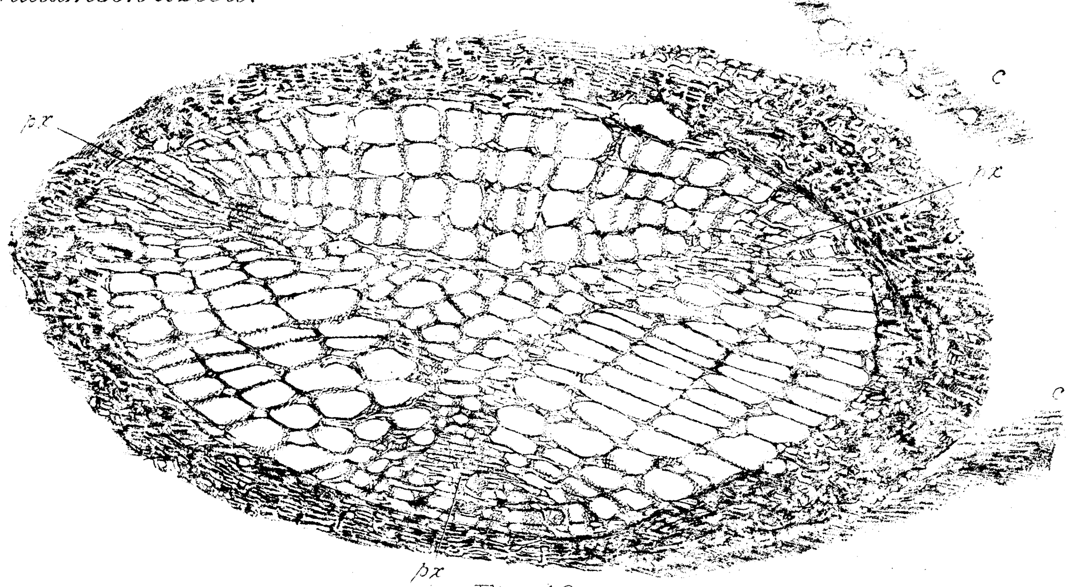


Fig. 40.

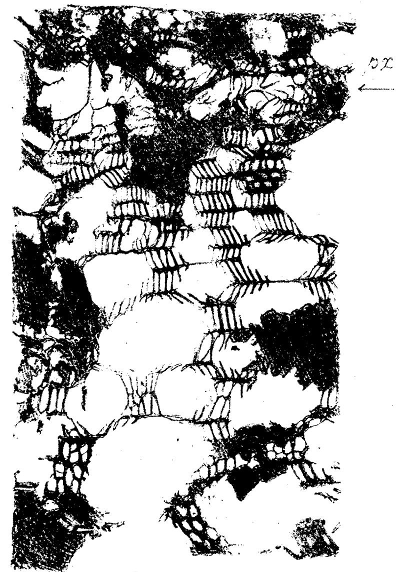


Fig. 41.

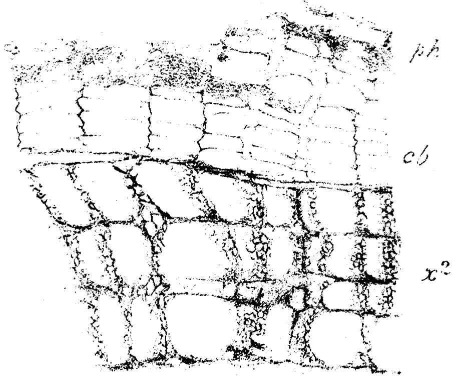


Fig. 42.

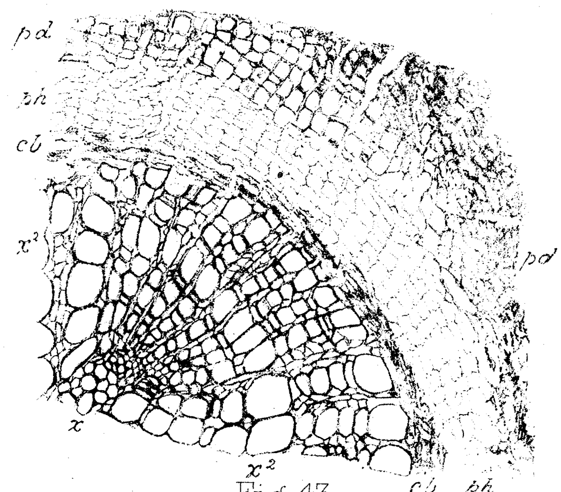


Fig. 43.

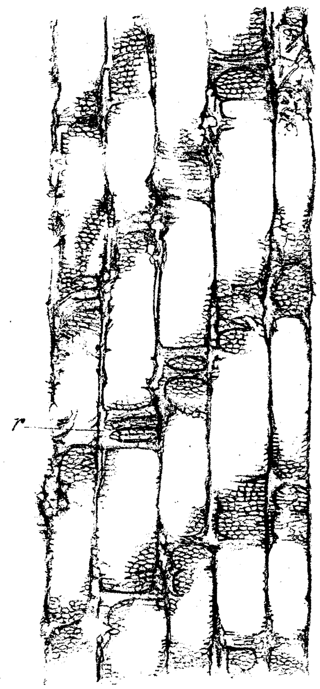


Fig. 44.

Fig. 44A.

Fig. 46.

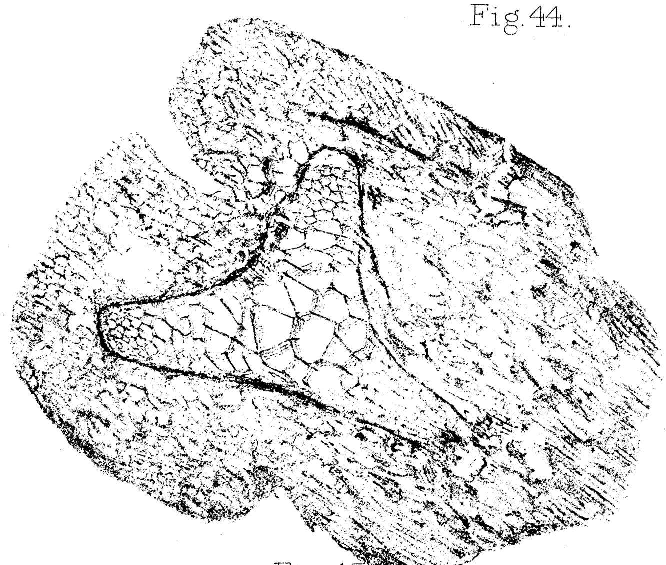


Fig. 45.

G. Brebner del.

Figs. 40—44A, Sphenophyllum plurifoliatum.
Figs. 45, 46, S. insigne.

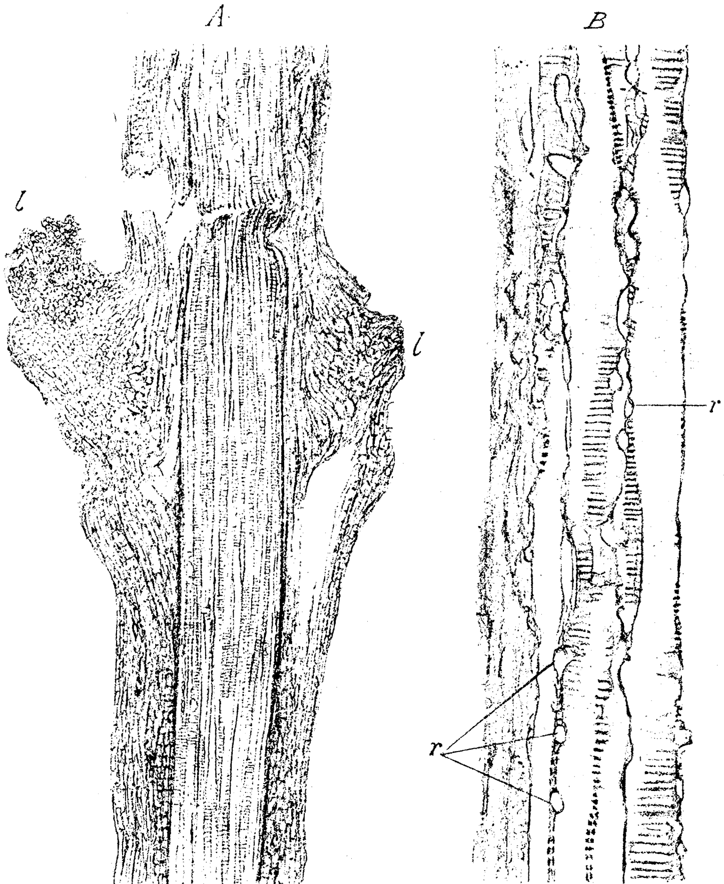


Fig. 47.

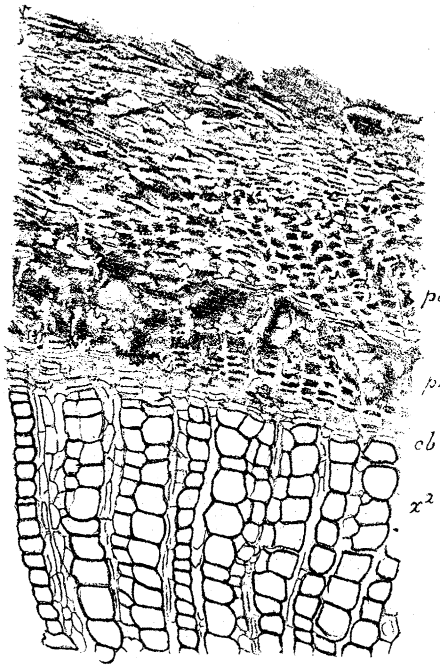


Fig. 48.

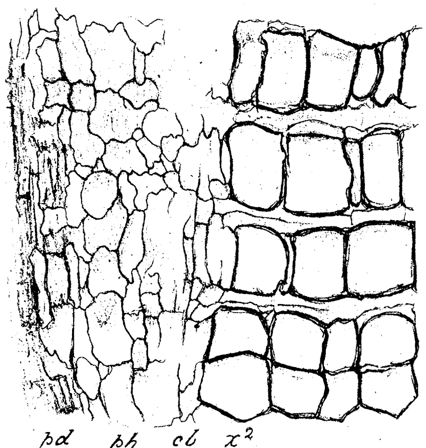


Fig. 51.

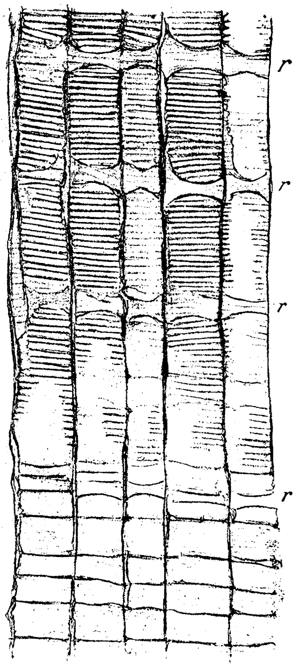


Fig. 49.

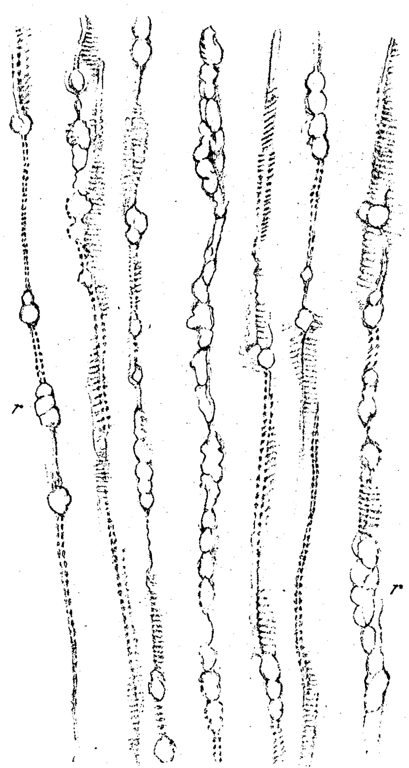


Fig. 50.

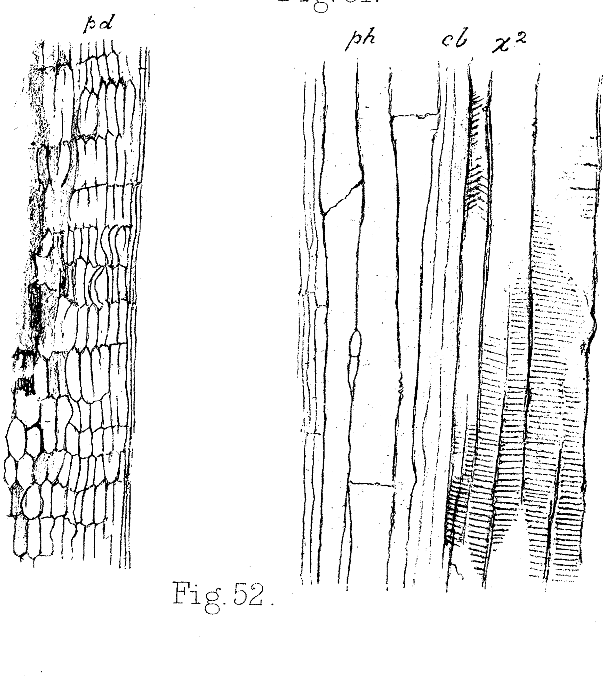


Fig. 52.

G. Brebner del.

Figs. 47—52, Sphenophyllum insigne.

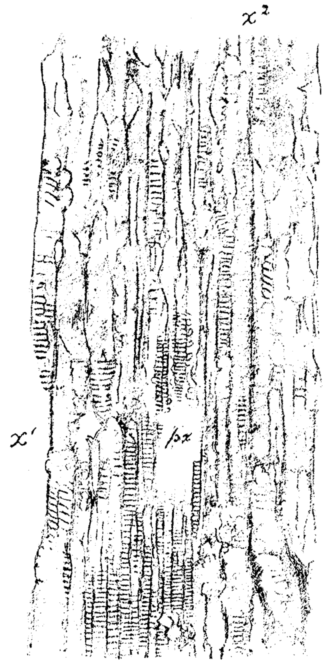


Fig. 53.

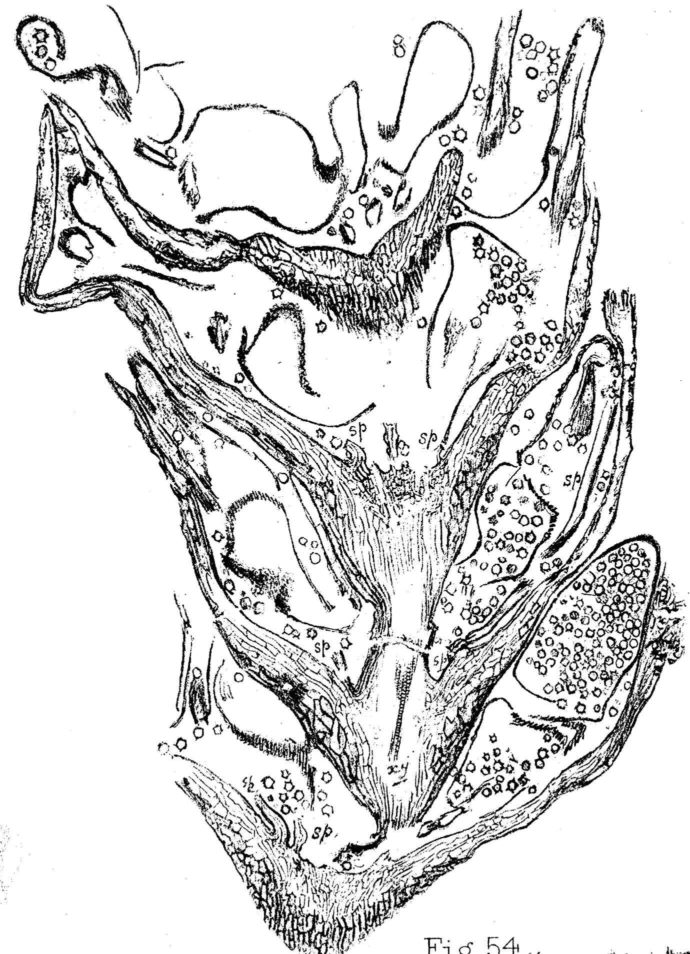


Fig. 54.

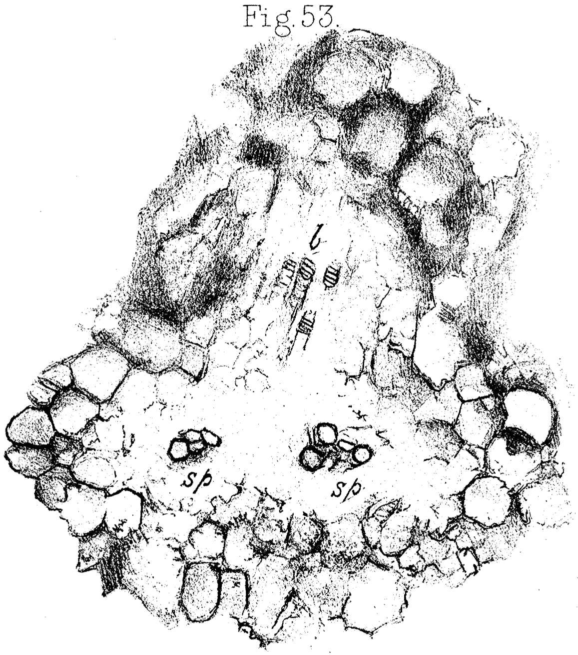


Fig. 55.

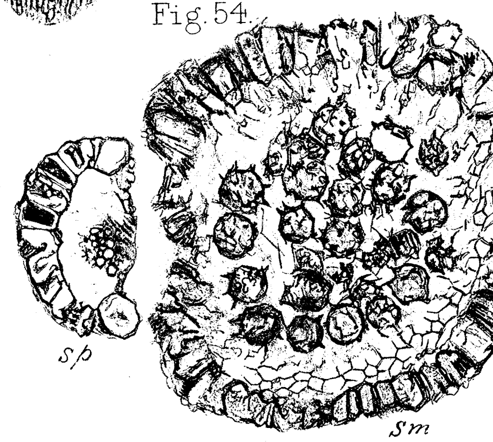


Fig. 57.

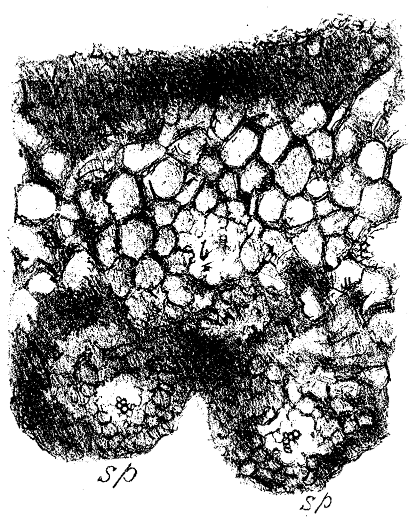


Fig. 56.

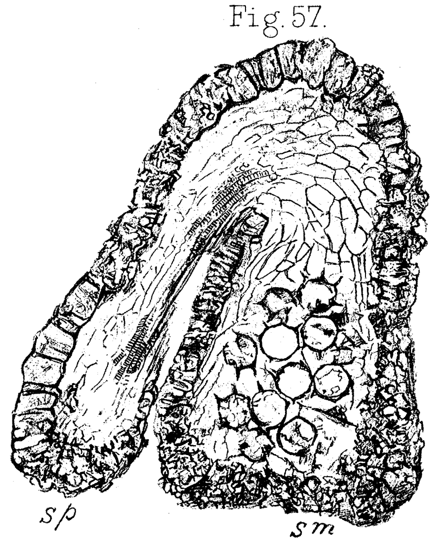
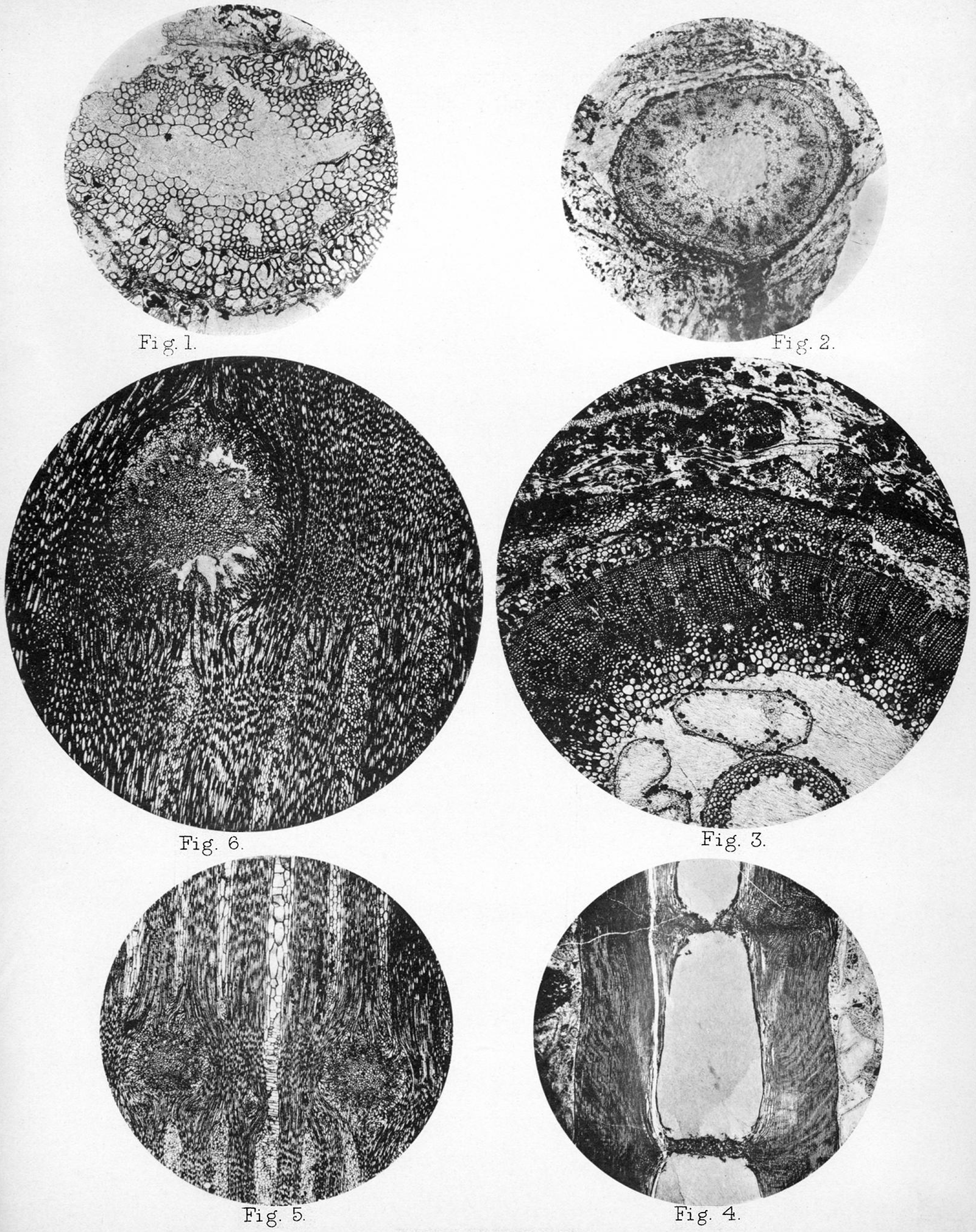


Fig. 58.

G. Brebner del.

Fig. 53, Sphenophyllum insigne.
Figs. 54–58, S. Dawsoni.

A—G, Calamites.



Figs. 1–6, Calamites.

PLATE 72.

Calamites.

Photograph 1. Transverse section of a very young twig, corticated. Seven vascular bundles are shown, each with a large canal on its inner side. Primary structure still unchanged. C.N. 1020. × about 60. See also Plate 77, fig. 2.

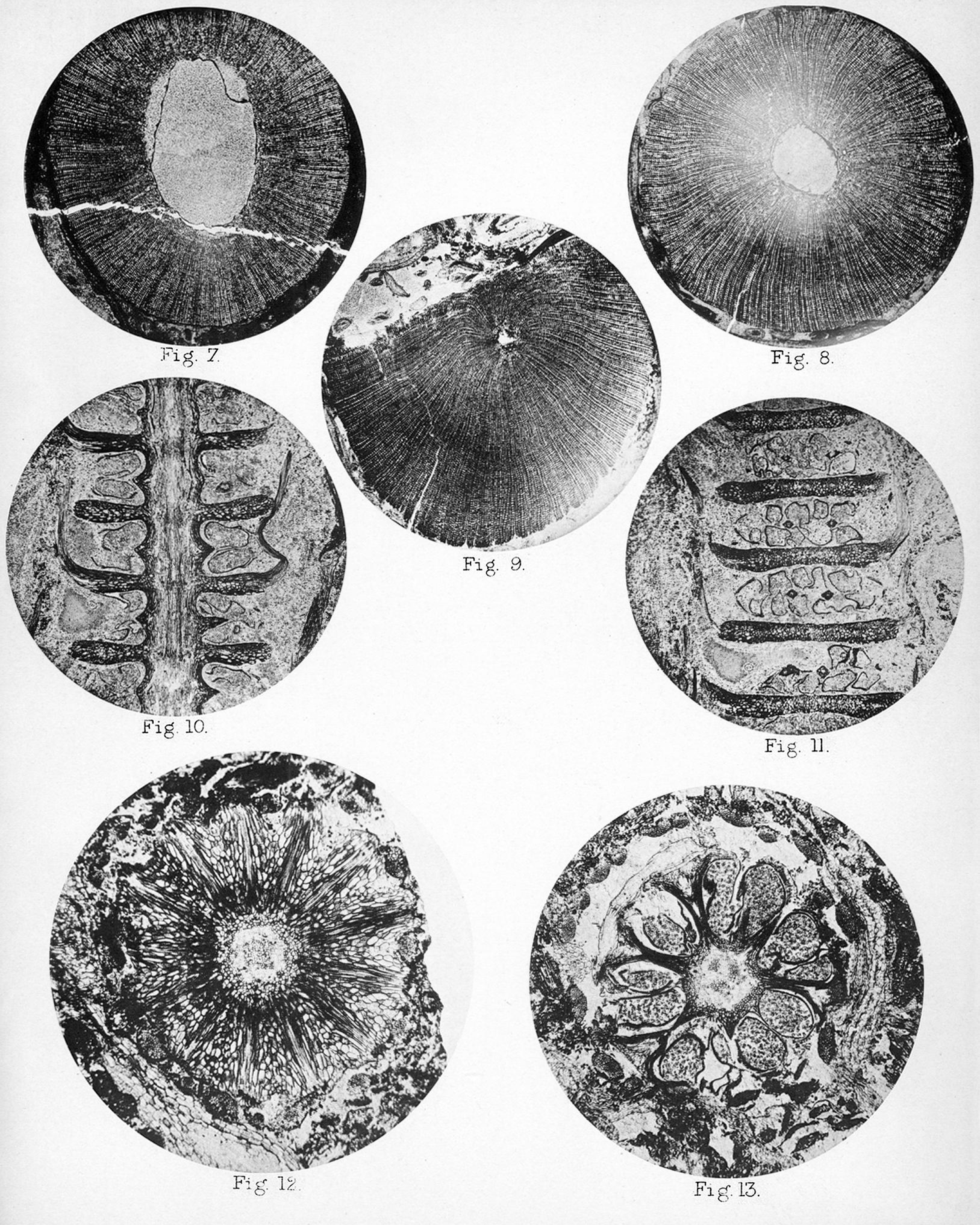
Photograph 2. Transverse section of a larger branch, with 19 vascular bundles; cortex well preserved. Several layers of secondary wood have already been formed. Outer part of the pith persistent. C.N. 1553. × about 15. See also Plate 77, fig. 3.

Photograph 3. Part of a transverse section of a larger branch, at a more advanced stage; seven of the vascular bundles (21 in all) are shown. Numerous layers of secondary wood have been formed. The cortex is differentiated into two layers. C.N. 118*. × about 25. See also Plate 78, figs. 12, 13, and 14.

Photograph 4. Radial section of part of a decorticated branch, showing two nodes, with their diaphragms. There is a considerable zone of secondary wood. Above the upper node, on the right hand, part of the base of a branch is shown. C.N. 1937. × about 9. From Mr. WILD's specimen.

Photograph 5. Tangential section through the wood of an advanced stem. The section passed through the inner part of the secondary wood. Five outgoing foliar bundles are seen in transverse section, as well as two branches out of the four which the complete section shows at this node. Observe that there is no regular alternation of the vascular bundles above and below the node. Observe the small-celled tissue of the medullary rays below the node. C.N. 130*. × about 12.

Photograph 6. Similar section of another specimen. This section has passed somewhat further towards the exterior. Several foliar bundles are shown, and one branch. Observe that its connection with the tracheæ of the main stem is chiefly from below. C.N. 1554. × about 12.



Figs. 7—9. Calamites.
Figs. 10—13. Calamostachys Binneyana.

PLATE 73.

Photographs 7, 8, and 9. *Calamites.*

Photograph 7. Transverse section of Mr. WILD's specimen, at some distance from the base of the branch, showing typical Calamitean structure, with a large pith-cavity, and 24 bundles, each with its canal. C.N. 1941. × about 10.

Photograph 8. Another section of the same, nearer the base. Pith-cavity much smaller, bundles normal, but only 14 in number. C.N. 1934. × about 10.

Photograph 9. Third section of the same, taken close to the base. Pith of minute size, with small irregular cavity, probably of *post-mortem* origin. Only 10 bundles, very crowded together, and with no distinct canals. C.N. 1933A. × about 10.

Photographs 10–13. *Calamostachys Binneyana.*

Photograph 10. Part of a radial section through a large strobilus. There are 18 whorls of bracts in the specimen, of which 4 are shown. Between them are the whorls of sporangiophores, of which 5 are shown, with their sporangia. Note the well-preserved central cylinder of the axis. C.N. 1022. × about 8.

Photograph 11. Part of a tangential section of the same specimen, showing the alternate whorls of coherent bracts, and of sporangiophores. In the former note the vascular bundles. The sporangiophores are seen in transverse section, each surrounded by its 4 sporangia. C.N. 1022A. × about 8. See also Plate 81, figs. 27 and 28.

Photograph 12. Transverse section passing through a whorl of coherent bracts, of which there are 13. Their vascular bundles can be seen. The small transverse sections, seen immediately outside the whorl, are those of bract-tips rising up from below. They alternate with the bracts of the next whorl. The still smaller transverse sections, seen in some places between the larger, are those of extreme tips of bracts from the second whorl below. C.N. 997. × about 20.

Photograph 13. Transverse section passing through a whorl of 6 peltate sporangiophores, some of which are shown completely, with the sporangium attached to the lower surface of the peltate expansion, at its edge. Here, again, the tips of the two whorls of bracts below are shown in transverse section surrounding the strobilus. C.N. 1020. × about 16.

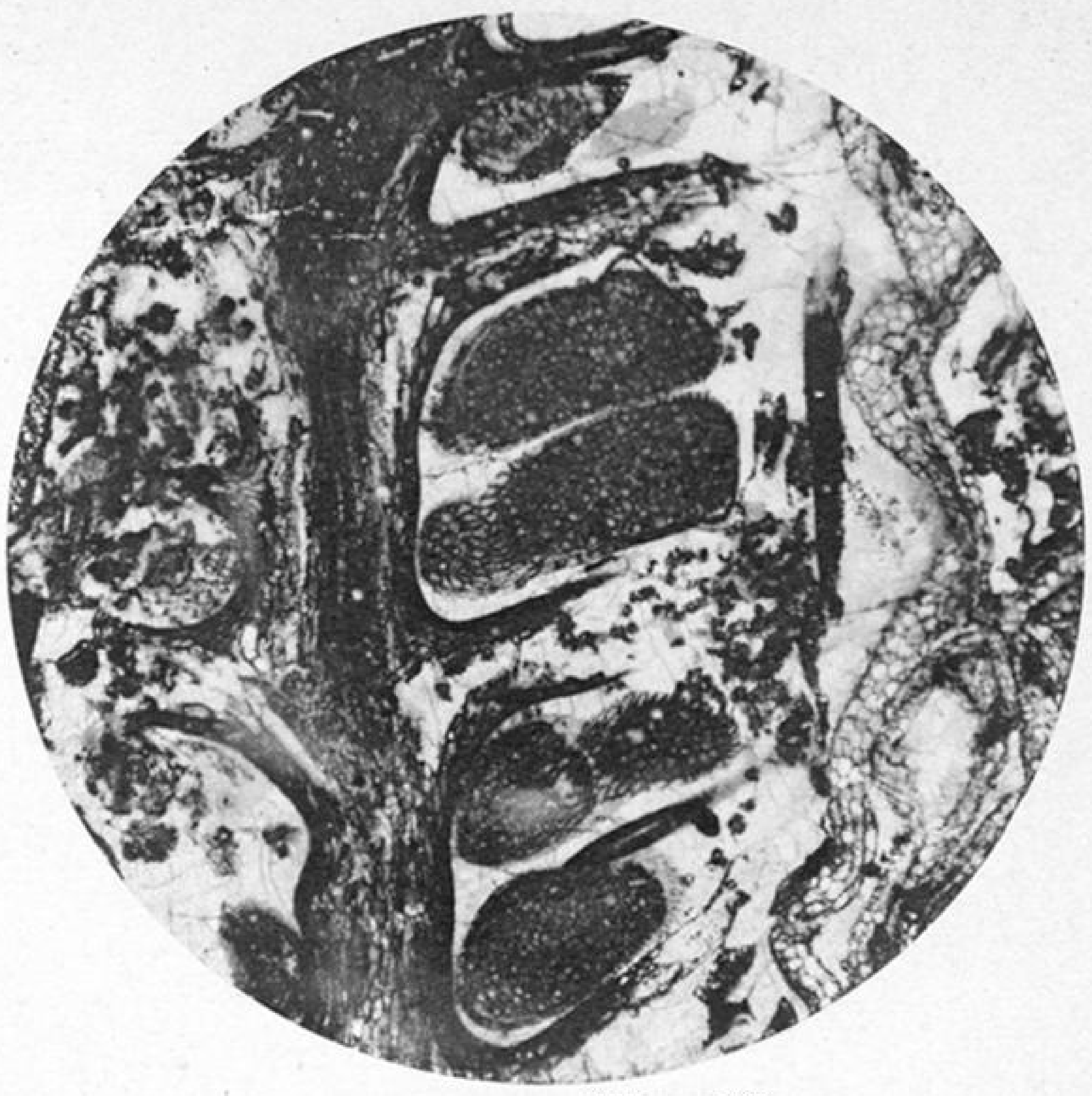


Fig. 17.

Fig. 14.

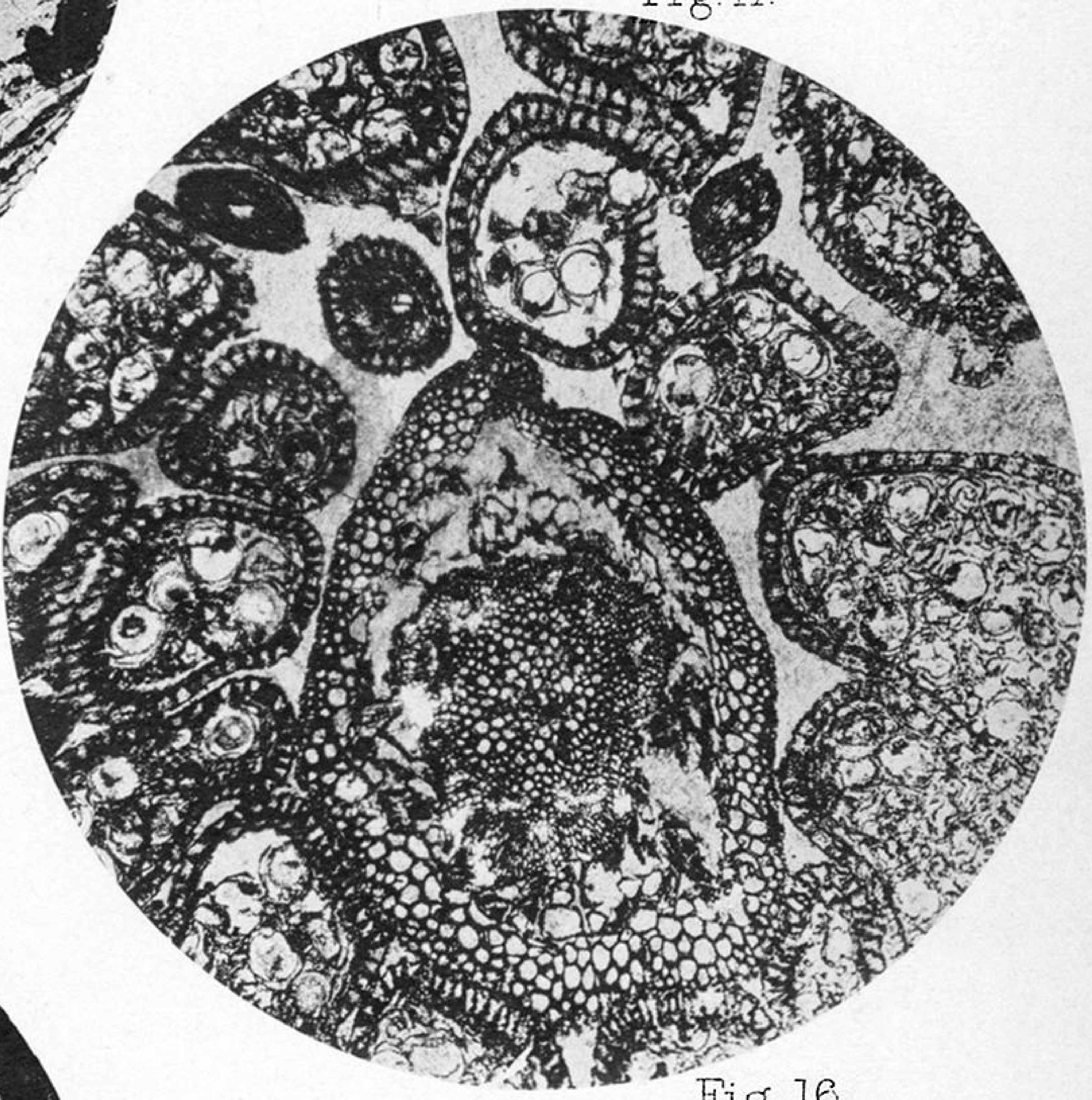


Fig. 16.

Fig. 15.

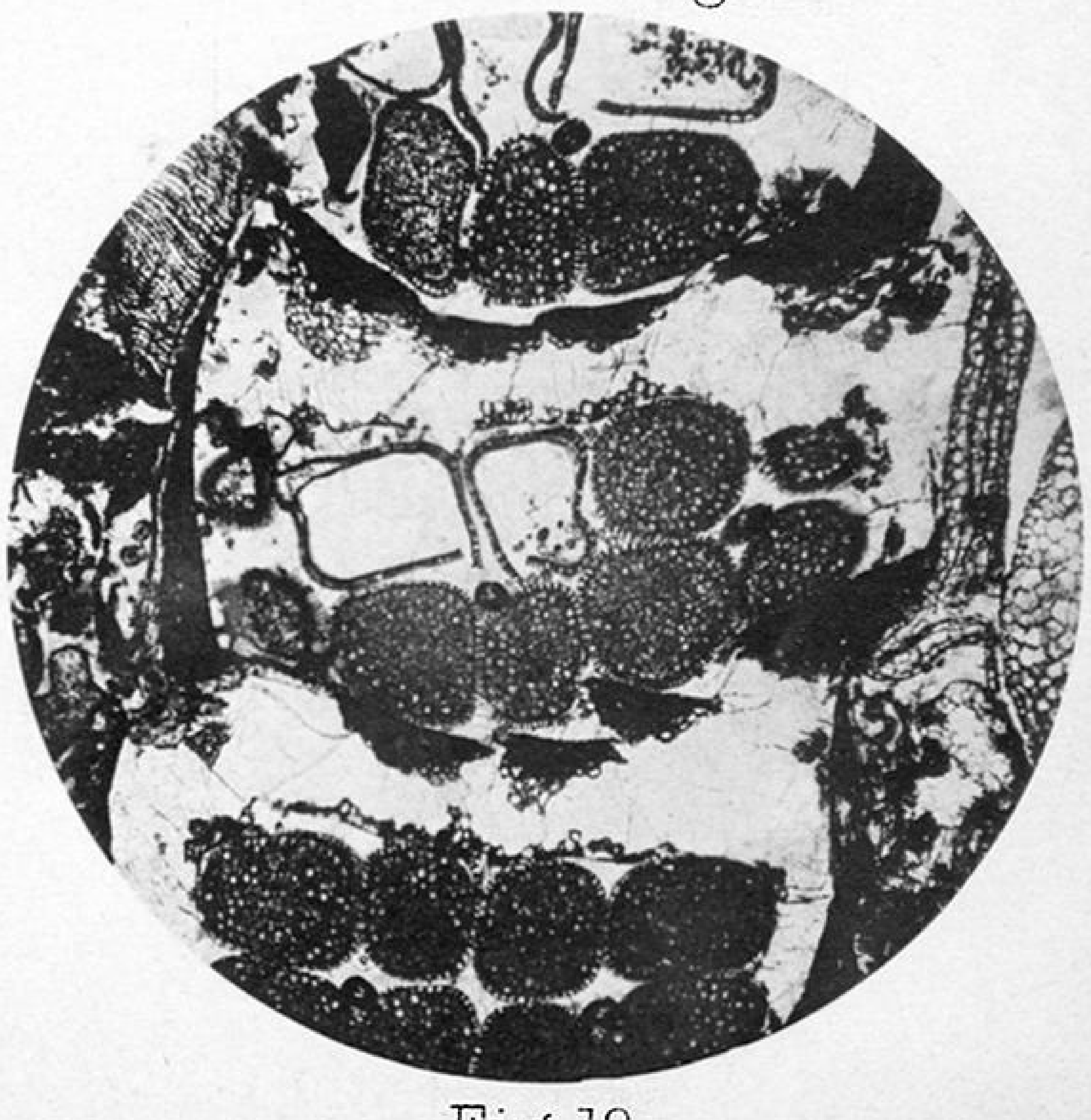


Fig. 18.

Fig. 14, Calamostachys Binneyana.
Figs. 15–16, C. Casheana. Figs. 17–18, Calamostachys sp.

PLATE 74.

Photograph 14. *C. Binneyana.* Transverse section of strobilus, passing through an internode. In the axis the stele has four prominent corners, with a bundle and its canal at each corner. A ring of sporangia surrounds the axis, and beyond these again are seen the extremities of bracts, some in section, others in surface-view. C.N. 1037A. × about 16.

Photograph 15. *Calamostachys Casheana.* Tangential section. Parts of three whorls are shown. All the sporangia are macrosporangia except one. The single microsporangium belongs to the middle whorl, and to a sporangiophore which also bears three macrosporangia. C.N. 1587. × about 18. See also Plate 82, fig. 38.

Photograph 16. Transverse section of the same specimen. Only macrosporangia are shown. The central cylinder has formed some secondary wood. C.N. 1588. × about 25. See also Plate 82, figs. 36 and 37.

Photograph 17. *Calamostachys sp.* Part of a radial section of the strobilus. The bracts and sporangiophores are obliquely ascending, not horizontal as in *C. Binneyana.* C.N. 1896. × about 8.

Photograph 18. Tangential section of the same specimen. C.N. 1897. × about 8.

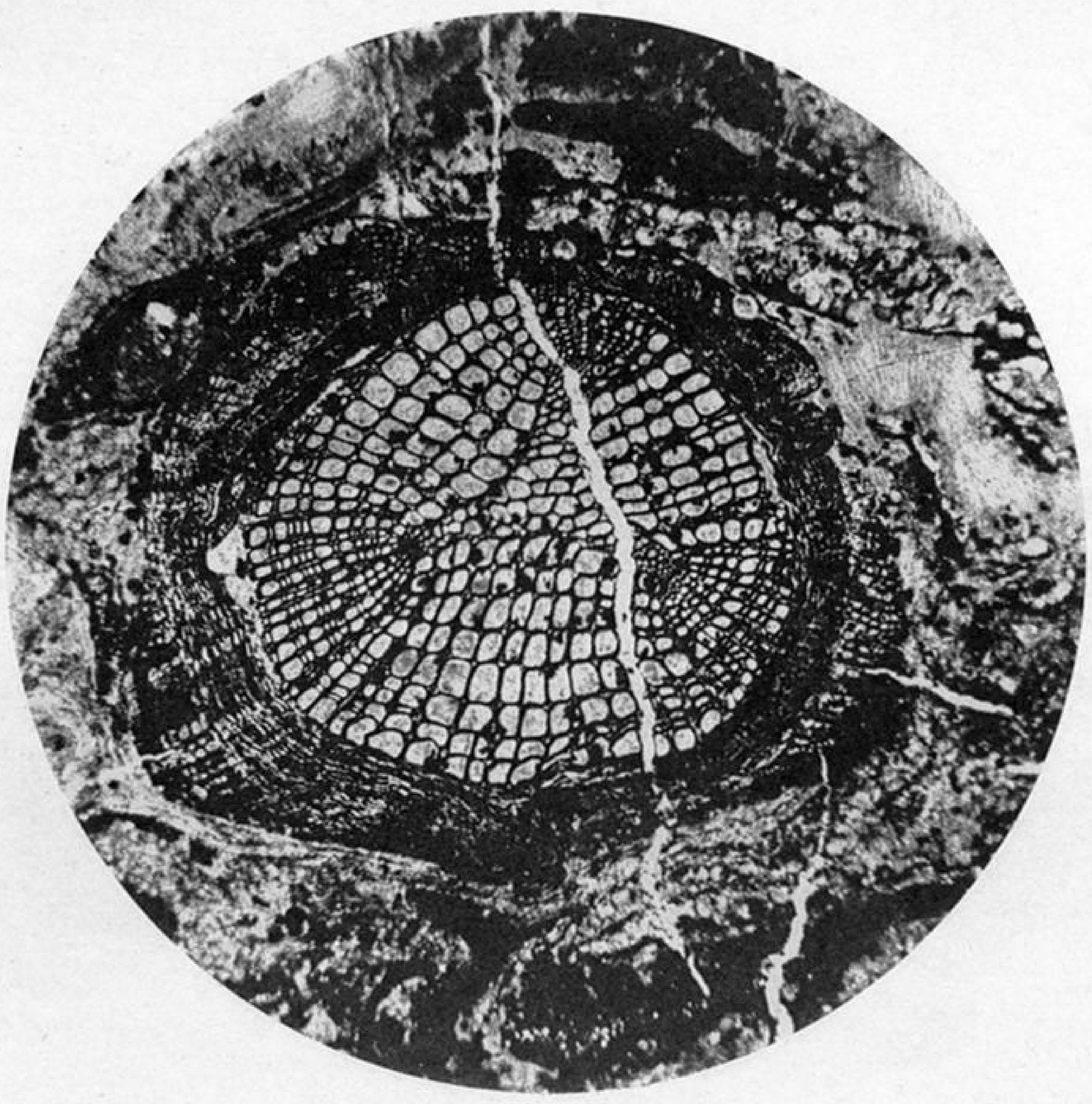


Fig. 19.

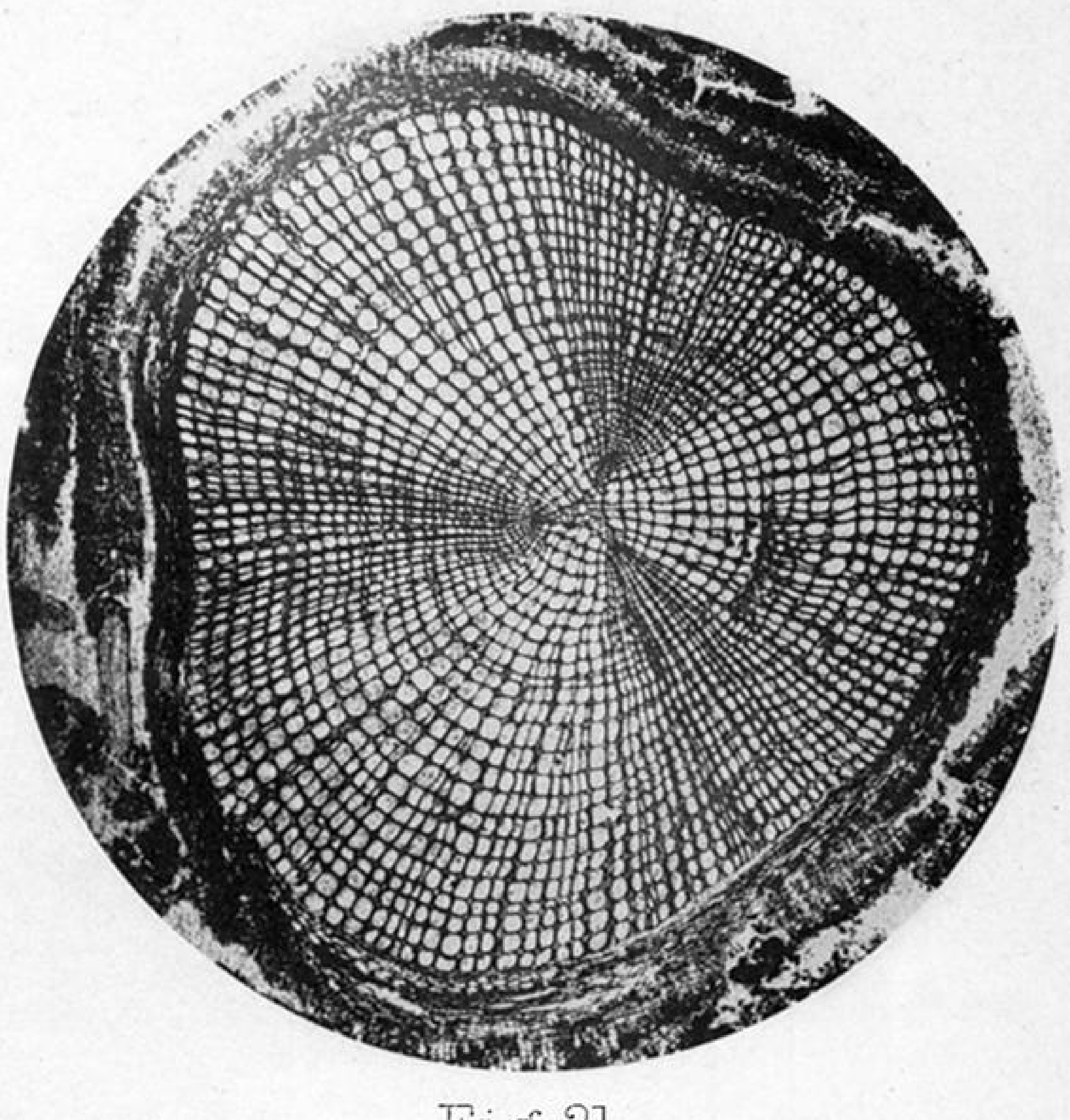


Fig. 21.

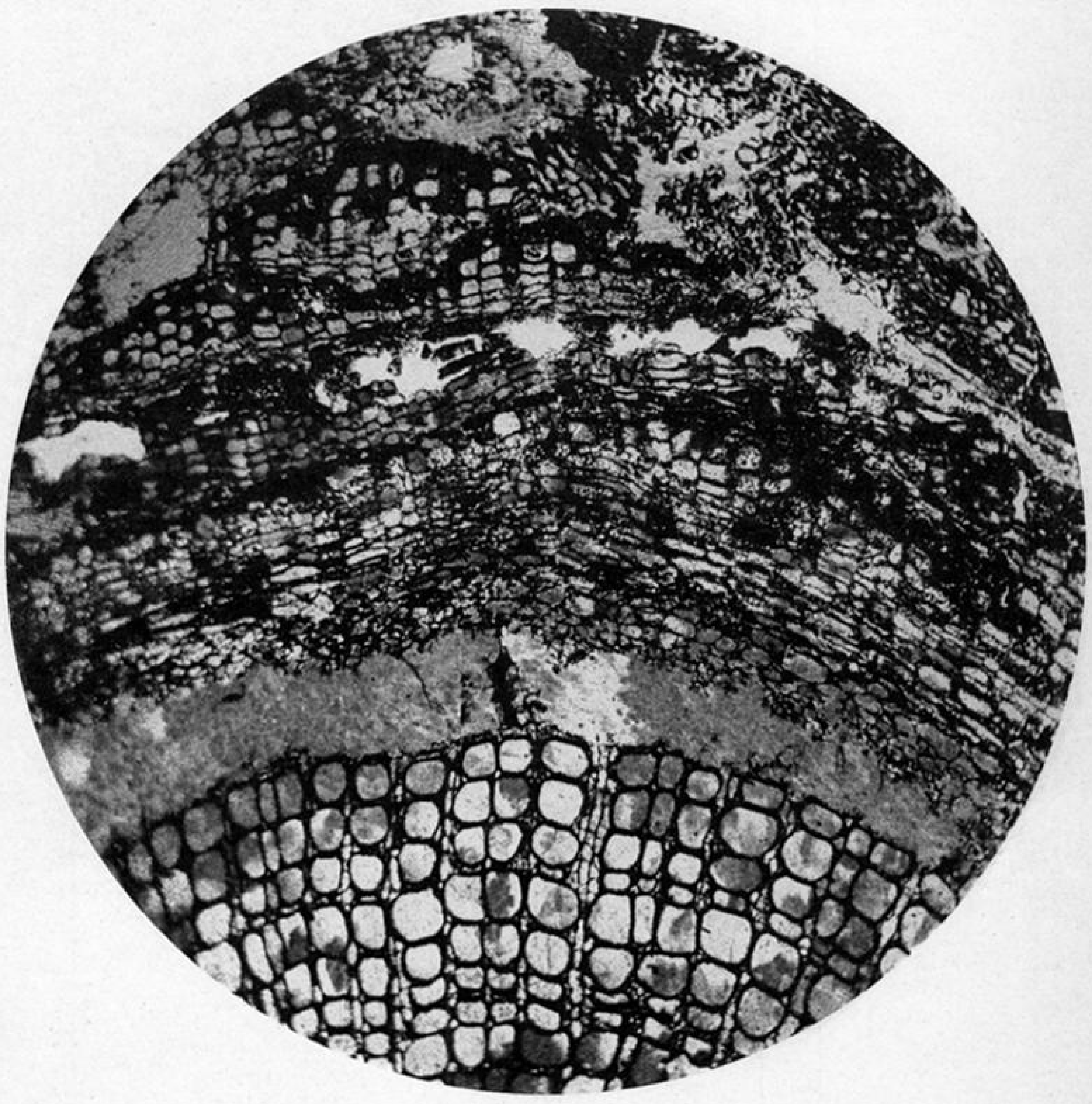


Fig. 22.

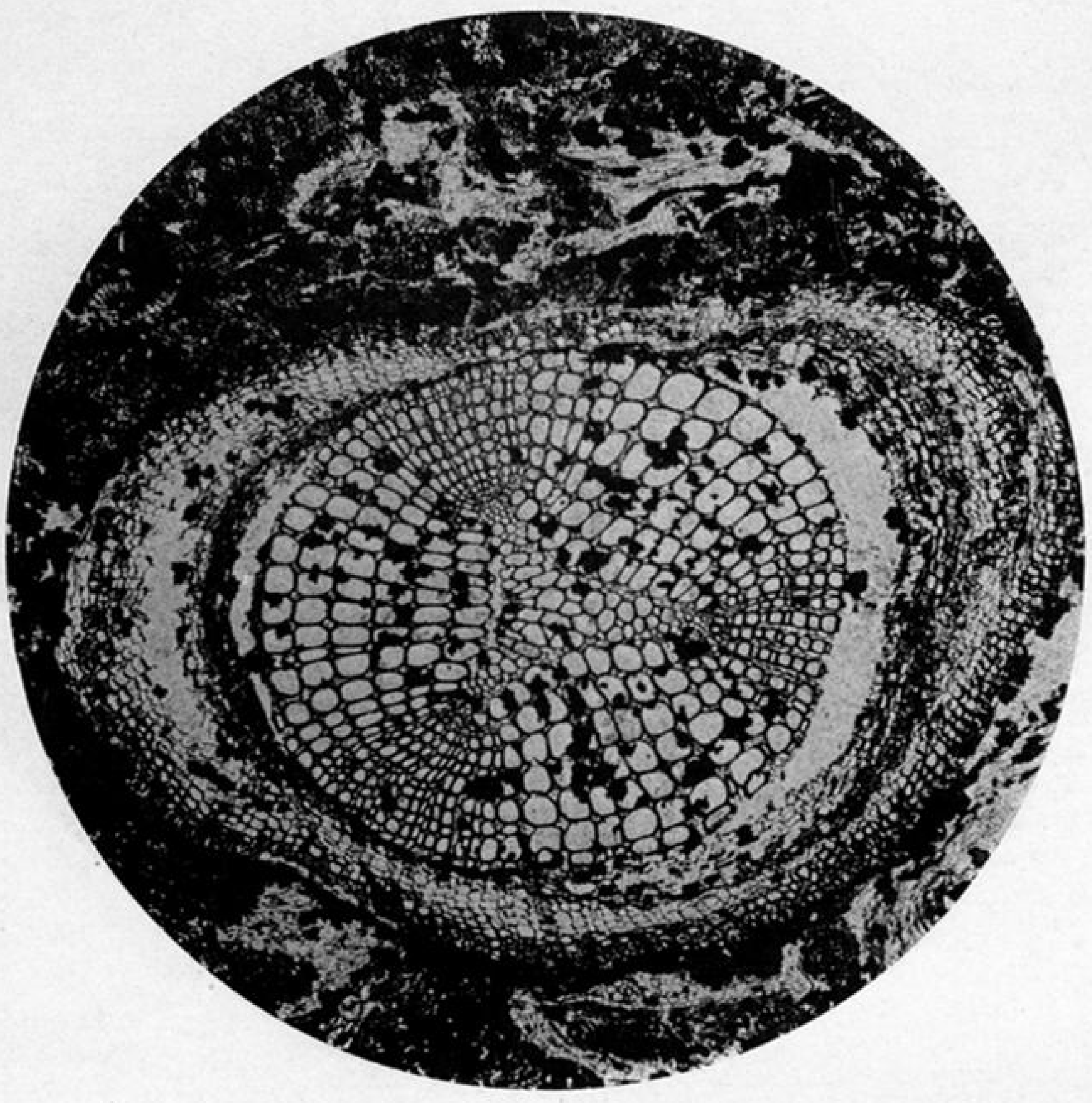


Fig. 20.

Figs. 19.—22. Sphenophyllum plurifoliatum.

PLATE 75.

Sphenophyllum plurifoliatum.

Photograph 19. Transverse section of a stem of moderate age, which has already cast off its primary cortex. The triarch primary xylem is shown; also the radially arranged fascicular and interfascicular secondary wood and, beyond that, the layers of phloëm and periderm. C.N. 894. × about 18. See also Plate 83, fig. 43.

Photograph 20. Transverse section of another stem at a similar stage. The details of the wood and of the periderm are especially clear. C.N. 899. × about 18.

Photograph 21. Transverse section of a very advanced stem. Structure of wood identical with that of previous specimens. To the exterior, successive scales of bark are shown. C.N. 1893. × about 8.

Photograph 22. Part of a transverse section of a still older stem, with secondary wood reaching 37 elements in thickness. Details of wood, especially xylem-parenchyma, very clear. Phloëm only partially preserved, but 4 successive layers of periderm are present. C.N. 901. × about 30.

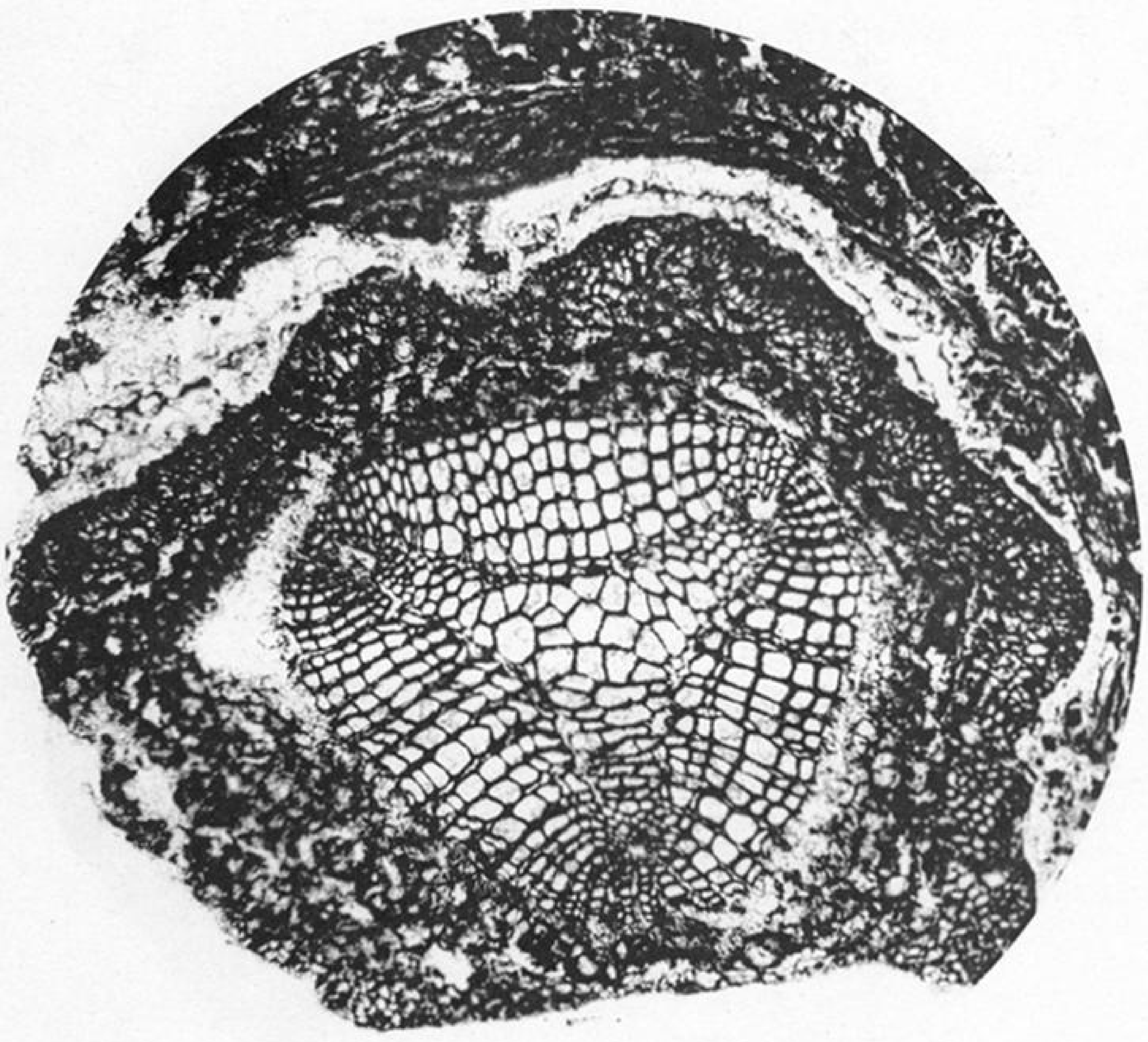


Fig. 23.

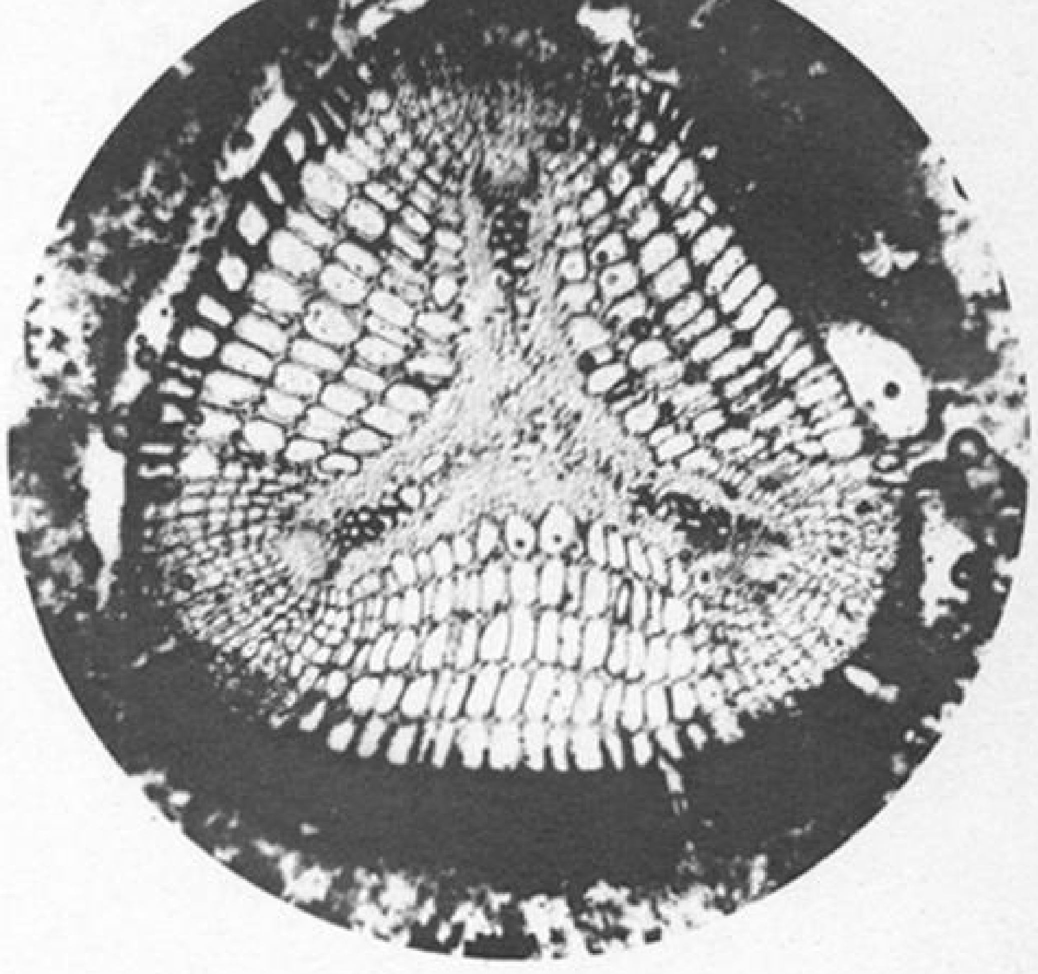


Fig. 24.

Fig. 26

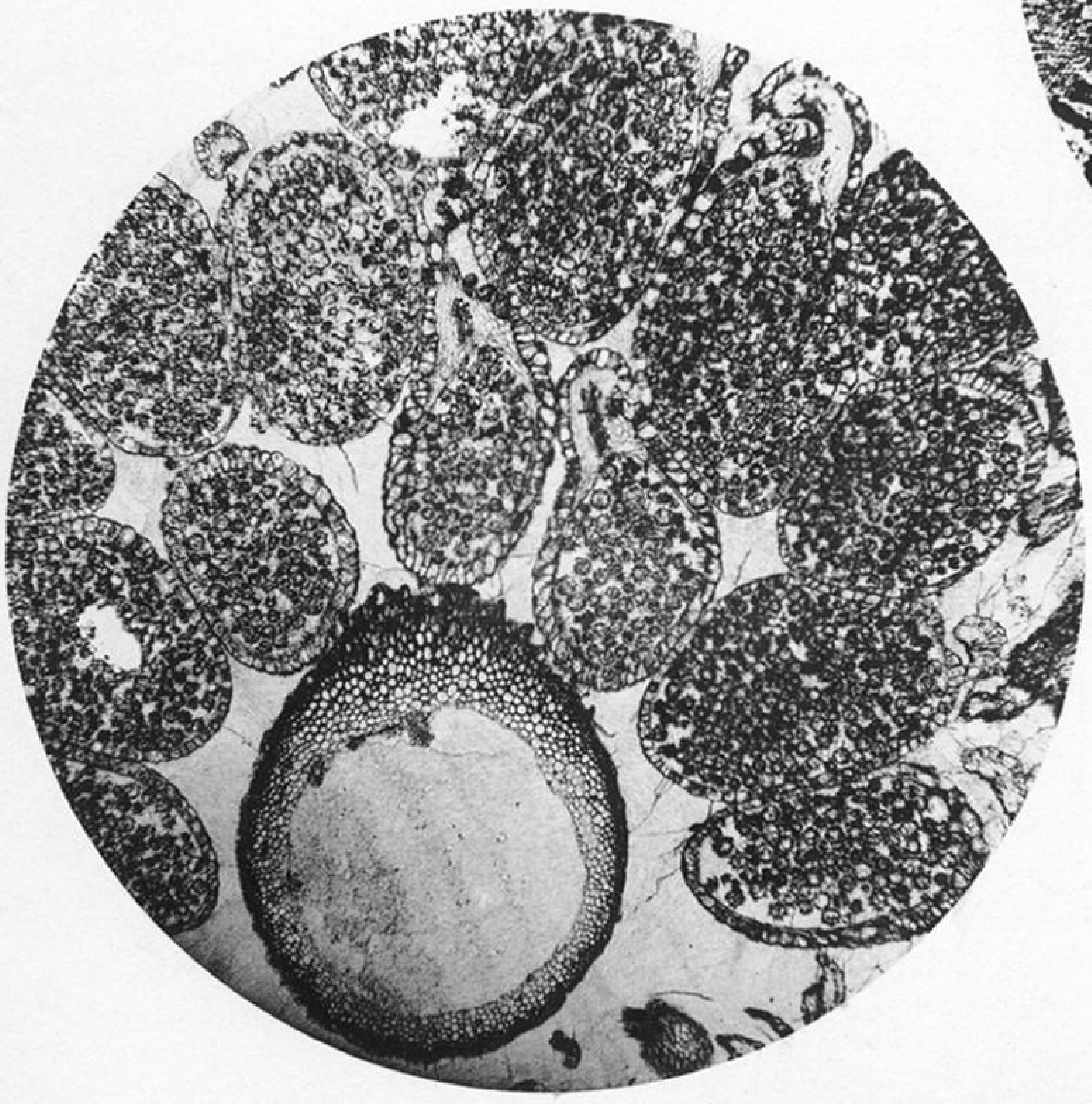


Fig. 25.

Fig. 23, Sphenophyllum insigne. Fig 24, Sphenophyllum sp.
Figs. 25-26 Sphenophyllum Dawsoni.

PLATE 76.

Photograph 23. *Sphenophyllum insigne.* Transverse section of a stem, which still retains its primary cortex. Triarch primary wood has a canal at each angle. 5–8 layers of secondary wood, with narrow medullary rays, have been formed. There are traces of periderm within the primary cortex. C.N. 919. × about 30.

Photograph 24. *Sphenophyllum* from Autun. Transverse section of a specimen presented by M. Renault. Observe the *hexarch* primary xylem, which is imperfectly differentiated towards the centre. Secondary wood as in *S. plurifoliatum.* C.N. 929. × about 12.

Photograph 25. Part of an approximately transverse section through the strobilus of *S. Dawsoni.* The central cylinder is absent, but leaf-trace bundles, within the cortex, are well shown. Several sporangia show attachment to sporangiophore, with its vascular bundle. C.N. 1898, H. × about 14.

Photograph 26. Approximately transverse section of a small strobilus of the same. The triangular xylem is shown in the axis. Part of the whorl of bracts seen is surface view, and sections of other bracts more to the exterior. One sporangium is shown attached to sporangiophore. C.N. 1898, I. × about 12.

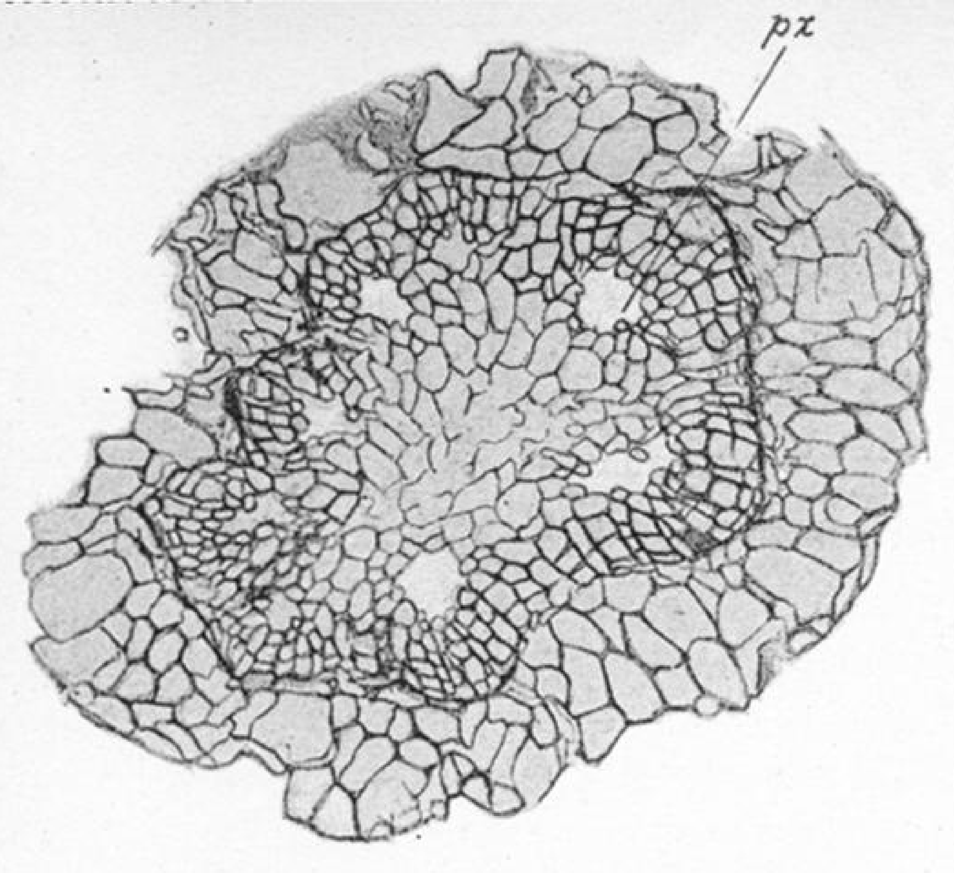


Fig. 1.

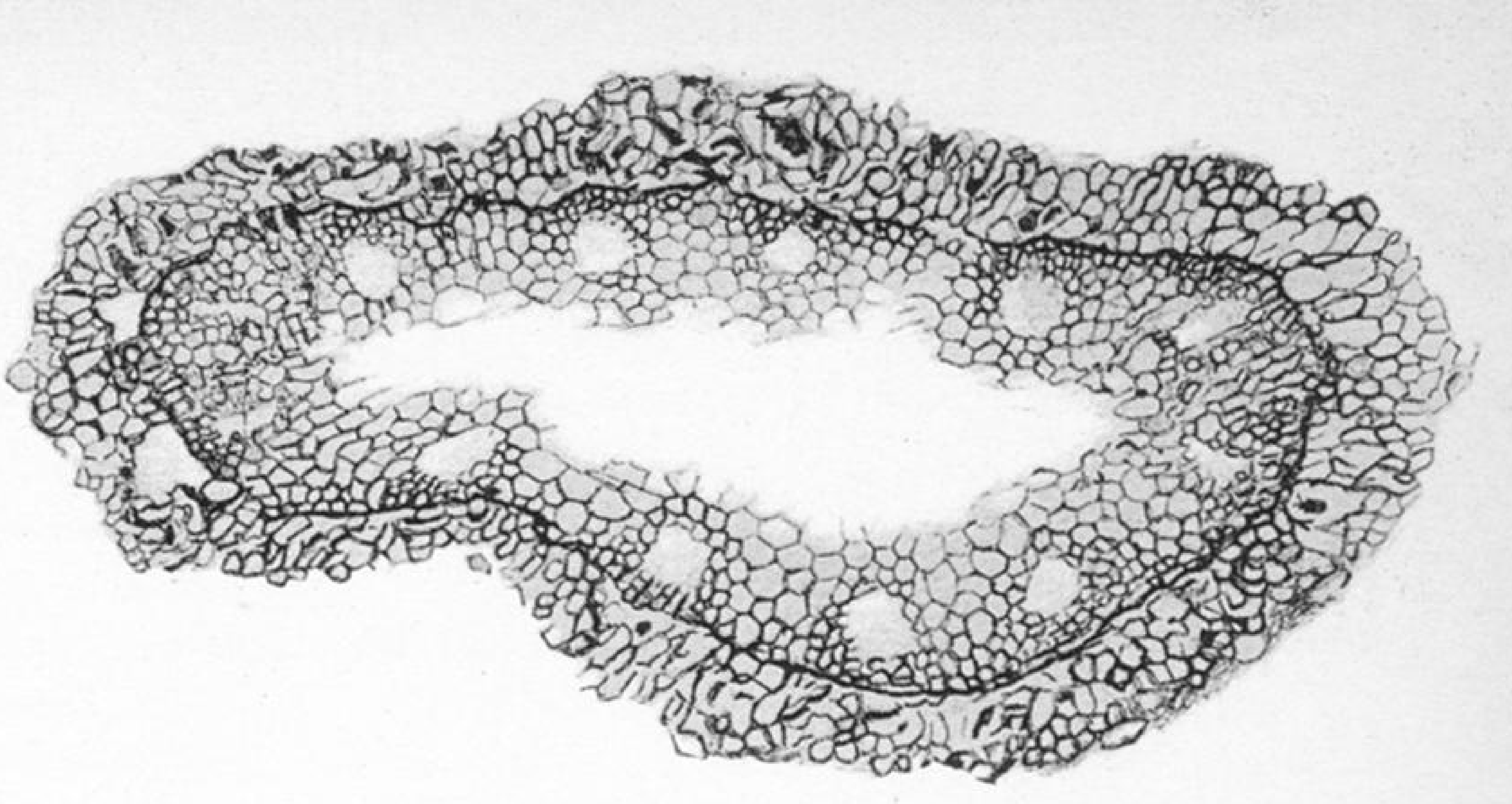


Fig. 2.

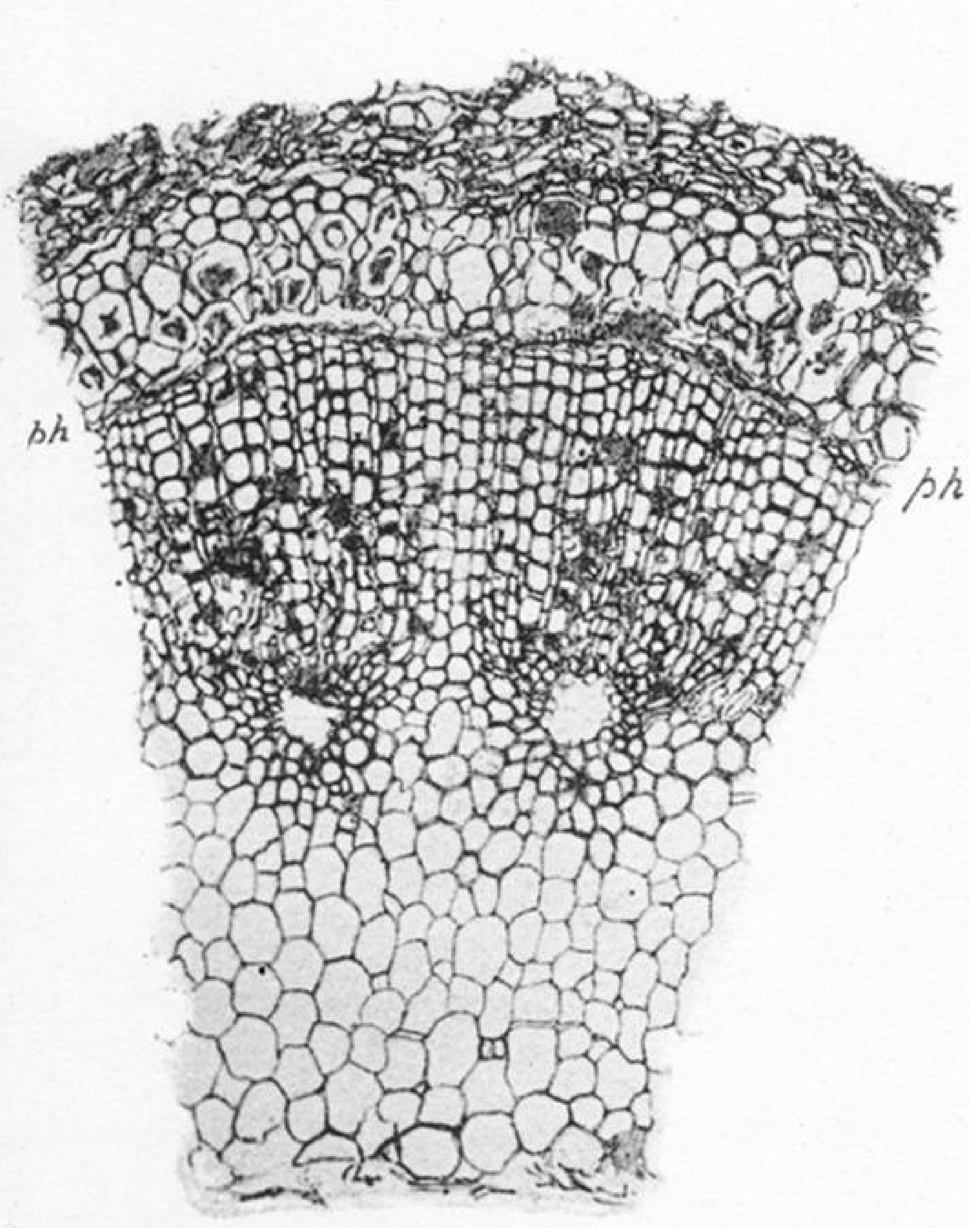


Fig. 3.

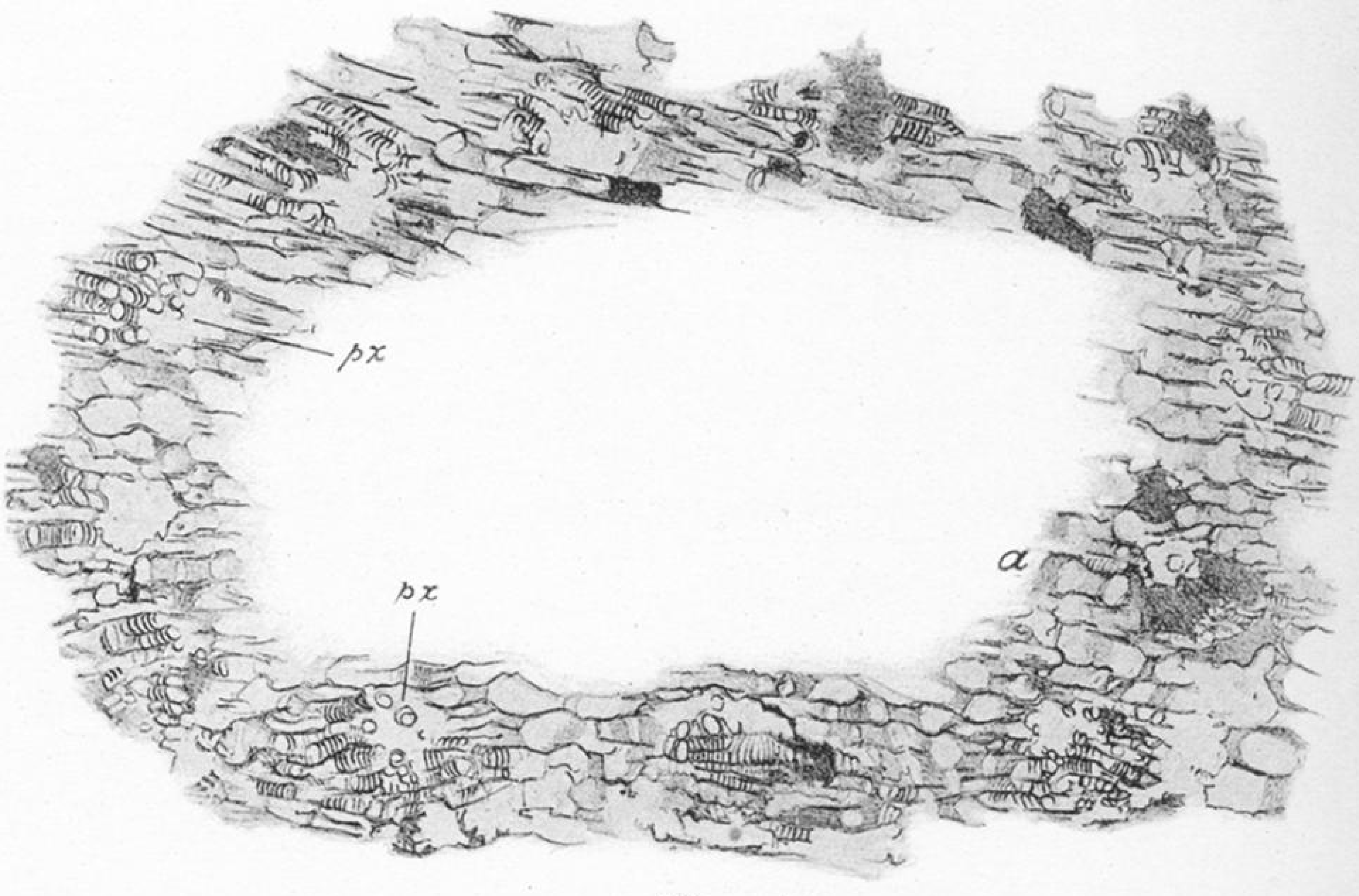


Fig. 4.

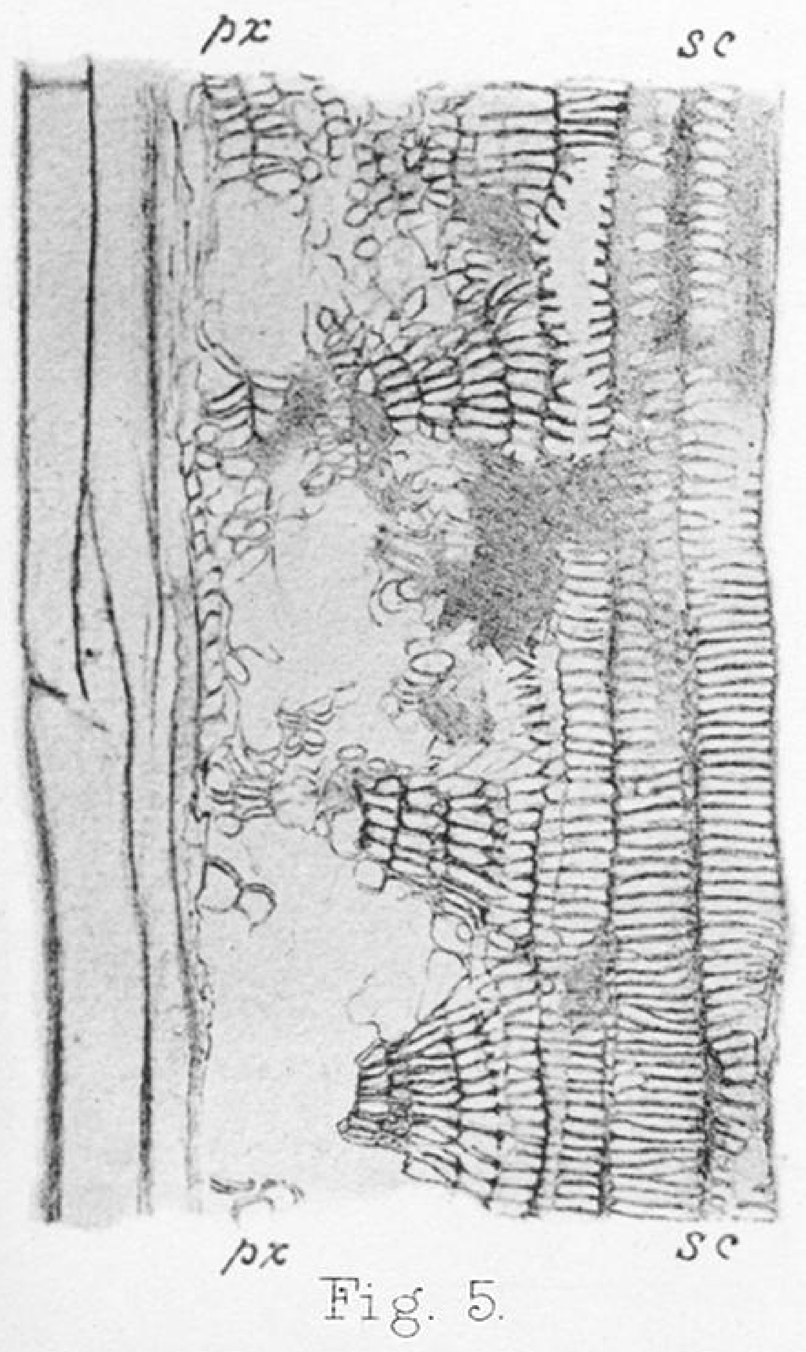


Fig. 5.

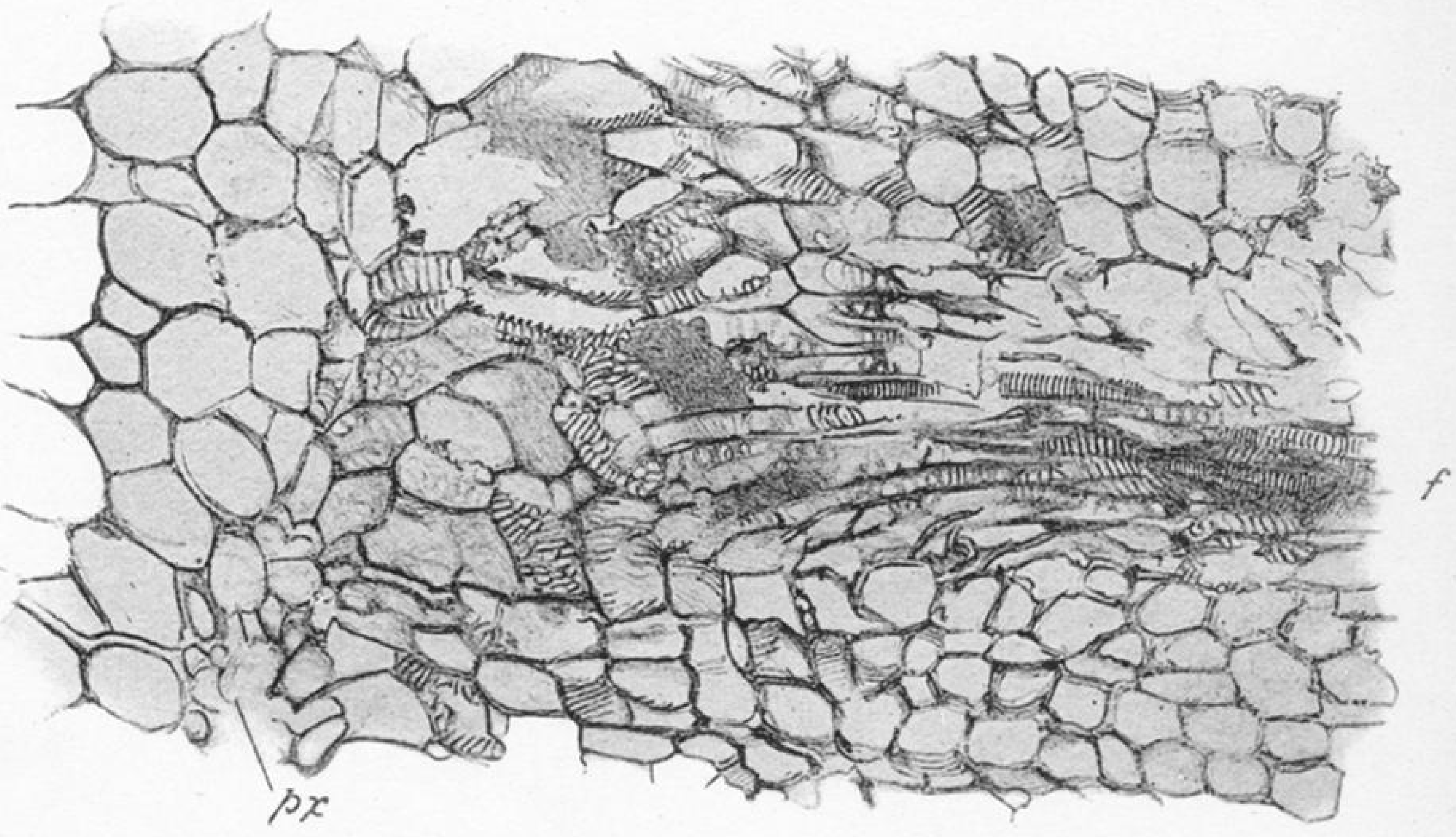


Fig. 6.

Figs. 1–6, Calamites.

PLATE 77.

Calamites.

Fig. 1. Transverse section of a very young twig. The pith is nearly solid, but slightly disorganized near the centre. There are seven vascular bundles, each with its canal. In most of the canals rings can be seen (as at *px*), which are the remains of the primitive tracheæ. Secondary wood, both fascicular and interfascicular, has just begun to be formed. The simple cortex is well preserved. C.N. 116*. × 100.

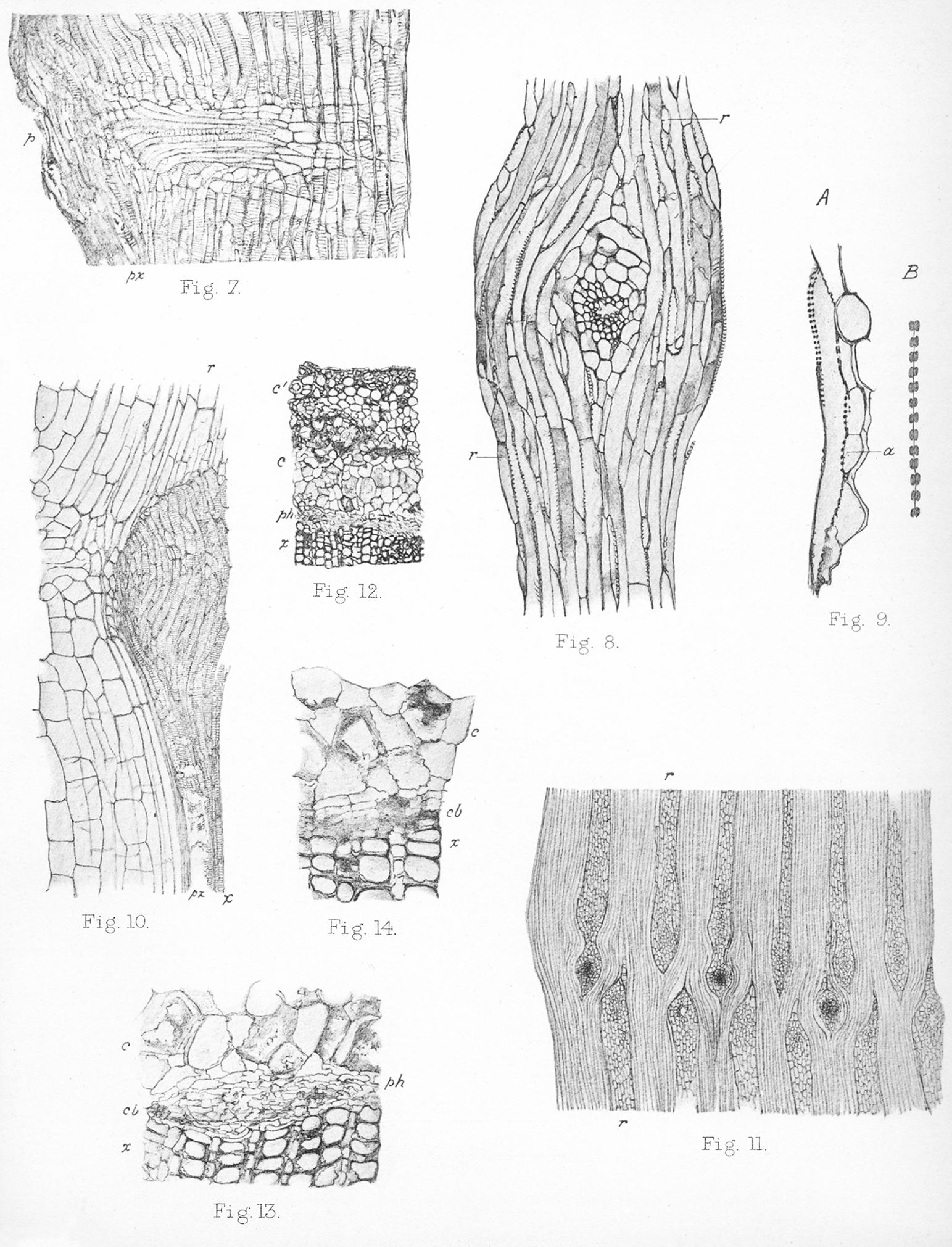
Fig. 2. Transverse section of a larger twig, but at a still earlier stage of development. The pith is hollow. There are twelve bundles, each with a canal, on the outer edge of which is the primary xylem. No secondary tissue has yet appeared. The cortex shows little differentiation. This is another section of the same specimen which is shown in Plate 72, photograph 1. C.N. 1561. × 50.

Fig. 3. Part of a transverse section of a larger and more advanced stem, the same as that of which another section is shown in Plate 72, photograph 2. A broad outer zone of pith is preserved. Two vascular bundles are shown. About twelve layers of secondary wood have been formed. The narrower elements belong to the secondary medullary rays. Interfascicular wood is already formed across the principal rays. The phloëm and cambium are disorganized, but their position is evident (*ph*). The well-preserved cortex is differentiated into two distinct layers. C.N. 14. × 50.

Fig. 4. Oblique section of a young branch; its cortex was preserved, but is not shown. The pith is hollow. There are twelve vascular bundles. In the canal of each bundle the fragmentary rings and spirals of the primitive tracheæ, or protoxylem, are seen, as at *px*. They sometimes extend to the inner margin of the canal (see especially the bundle marked *a*). Only the primary xylem of the bundles exists at this stage. C.N. 1002. × 100.

Fig. 5. Part of a radial section passing through the primary wood of a bundle. On the left are pith-cells. In the middle is the canal, which is still partly filled by the disorganized remains of the protoxylem (*px*). The tracheæ are partly annular, partly spiral. Towards the right they become more continuous. Still further to the right we see the persistent scalariform tracheæ (*sc*) of the primary wood external to the canal. C.N. 20A. × 200.

Fig. 6. Part of a transverse section, showing a leaf-trace bundle passing out horizontally through the secondary wood. On the left are pith-cells; *px*, protoxylem of a bundle passing into the next internode. The reticulated tracheæ belong to the nodal wood. The tracheæ of the foliar bundle, *f*, are spiral and scalariform. C.N. 118*. × 150.



Figs. 7–14, Calamites.

PLATE 78.

Calamites.

Fig. 7. Part of a radial section, showing a leaf-trace bundle passing out through the nodal and secondary wood; disorganized pith (*p*) is on the left. The nodal wood can be distinguished by its short tracheæ. The leaf-trace consists of tracheæ (on some of which the spiral thickening is seen) and surrounding parenchyma. The section not being quite in the plane of the outgoing bundle, the latter appears to die out towards the right. *px*, protoxylem of bundle below the node. C.N. 22 × 100.

Fig. 8. Part of a tangential section, showing a leaf-trace bundle cut transversely. The section passes through the inner part of the secondary wood. The pitting is almost entirely confined to the radial walls of the tracheæ. The shaded parts of the latter represent the unpitted tangential walls; the parts left white are in section; several secondary rays are shown (as at *r*). Some of the tracheæ show traces of transverse septa, but most of these appearances are due to oblique section of their tangential walls. The leaf-trace has a gap, where some of its primitive tracheæ are disorganized. It is surrounded by parenchyma. C.N. 20B. × 100.

Fig. 9. *A*. Short tracheide and neighbouring cells, in tangential section, to show bordered pits. Towards the parenchyma the border is unilateral (as at *a*). C.N. 20A (same specimen as 20B, but from a section nearer the pith). × 200.
B. Wall between two tracheæ, to show bordered pits, in tangential section. C.N. 1554 (shown in Plate 72, photograph 6). × 500.

Fig. 10. Part of radial section, passing through a node. The pith is to the left. Above the node part of a primary ray (*r*) is shown. The canal of a bundle, containing remains of the protoxylem (*px*) passes up to the node from below. The protoxylem is continuous with the innermost elements of the nodal wood. The rest of the nodal wood is continuous with the persistent primary xylem (*x*) immediately outside the canal. C.N. 21. × 50.

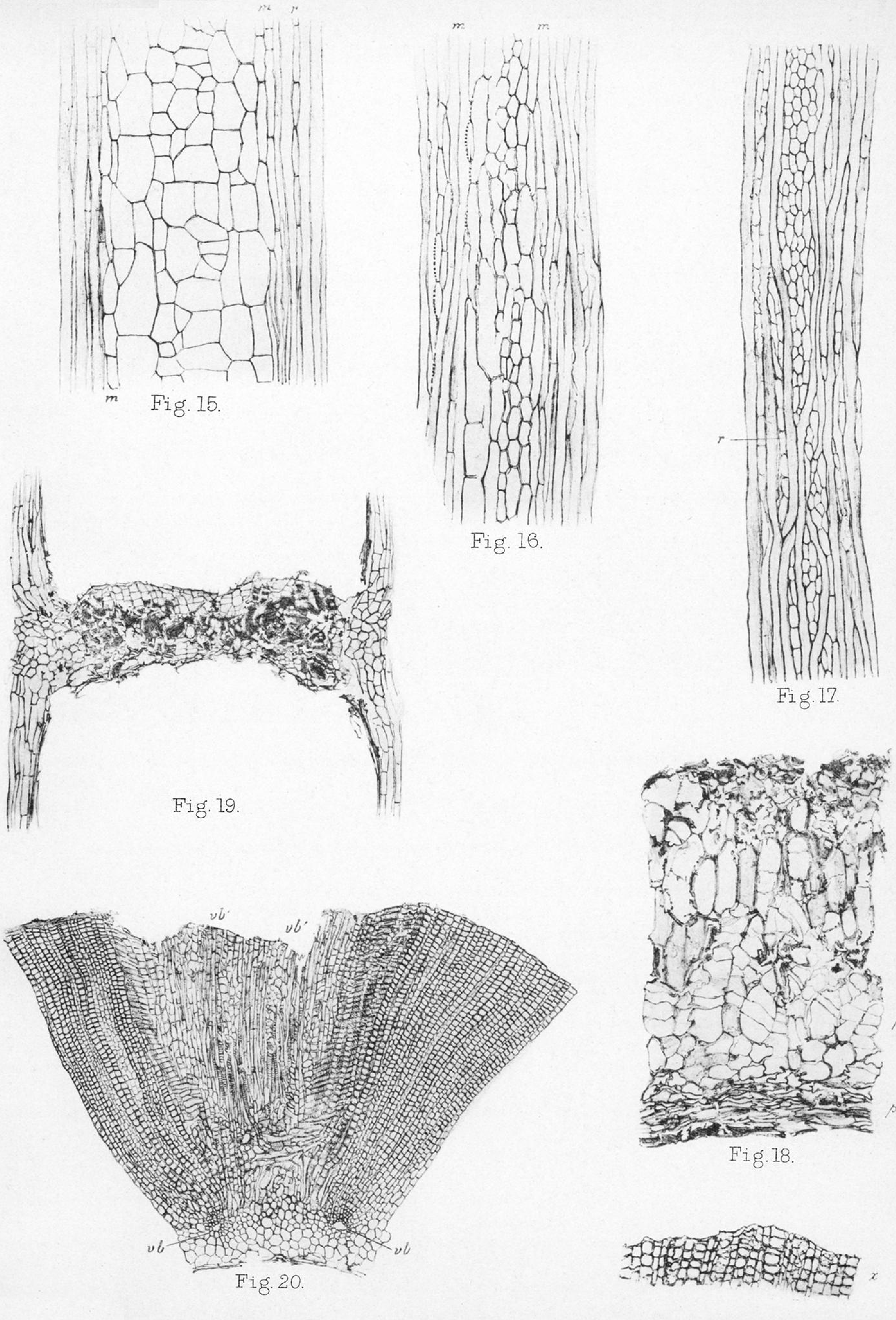
Fig. 11. Tangential section, to show course of vascular bundles. Three outgoing leaf-trace bundles are shown, in transverse section, at the node. Only the alternate bundles pass out at this node; the intermediate bundles do not pass out, but fork and attach themselves to the neighbouring strands. The relatively broad, small-celled rays (as at *r*) show that the section passes near the pith. C.N. 26. × 13.

Fig. 12. Part of transverse section, showing cortex and outer layers of wood (*x*). Remains of the phloëm (*ph.*) are seen. The cortex consists of two distinct layers (*c* and *c'*); the outer layer becomes more sclerenchymatous towards the periphery. C.N. 118*. × 50.

Fig. 13. Another part of the same section showing a phloëm-group (*ph*). The cambium (*cb*) between wood and phloëm is also preserved, and the phloëm itself is complete, though crushed. The large cells above belong to the cortex (*c*) C.N. 118*. × 150.

Fig. 14. From the same section, showing a small portion of wood (*x*), cambial cells (*cb*) and their derivatives, and cortex (*c*). C.N. 118*. × 150.

The figs. 12, 13, and 14 are from the section, a part of which is shown in Plate 72, Photograph 3.



Figs. 15—20. Calamites.

PLATE 79.

Calamites.

Fig. 15. Tangential section passing through a principal medullary ray near the pith. On either side are seen tracheides and one or two secondary rays (as at *r*). The principal ray is entirely parenchymatous; the elements towards the middle are quite short; those near the edges are narrower and more elongated (*m*). C.N. 65. × 50.

Fig. 16. From another section of the same stem, showing a principal ray further towards the exterior. The whole ray is narrower; the marginal cells (*m*) are more elongated, and are already partly replaced by tracheides. The ray to the left (*r*) may probably have been cut off from the principal ray by interpolated tracheides. C.N. 66. × 50.

Fig. 17. A third section of the same stem, still further towards the exterior. The principal ray is no longer continuous, but is completely broken up by interpolated tracheides. Some of its isolated parts (*r*) are quite similar to secondary rays. C.N. 67. × 50.

Fig. 18. Part of a transverse section showing cortex, and a small part of the secondary wood (*x*); the gap between them was caused by the growth of a Stigmarian rootlet, which is not figured. Remains of the phloëm (*ph*, are shown. Many of the cortical cells, especially those at a short distance from the interior, show recent tangential divisions, indicating the formation of periderm (*pd*). From a slide (No. 6) prepared by Mr. Lomax, in the possession of D. H. Scott. × 70.

Fig. 19. Part of a median section, passing through a diaphragm. The cells towards both surfaces of the diaphragm have undergone regular tangential divisions (best shown on the upper surface), forming a layer of periderm. C.N. 132***. × 30.

Fig. 20. Part of a transverse section passing tangentially through the base of a branch, which is inserted between two bundles (*v.b.*) of the main stem. The primary vascular bundles (*v.b′.*), and interfascicular tissue of the branch are shown, and the connections with the wood of the main stem. C.N. 132** (from same stem as the last). × 30.

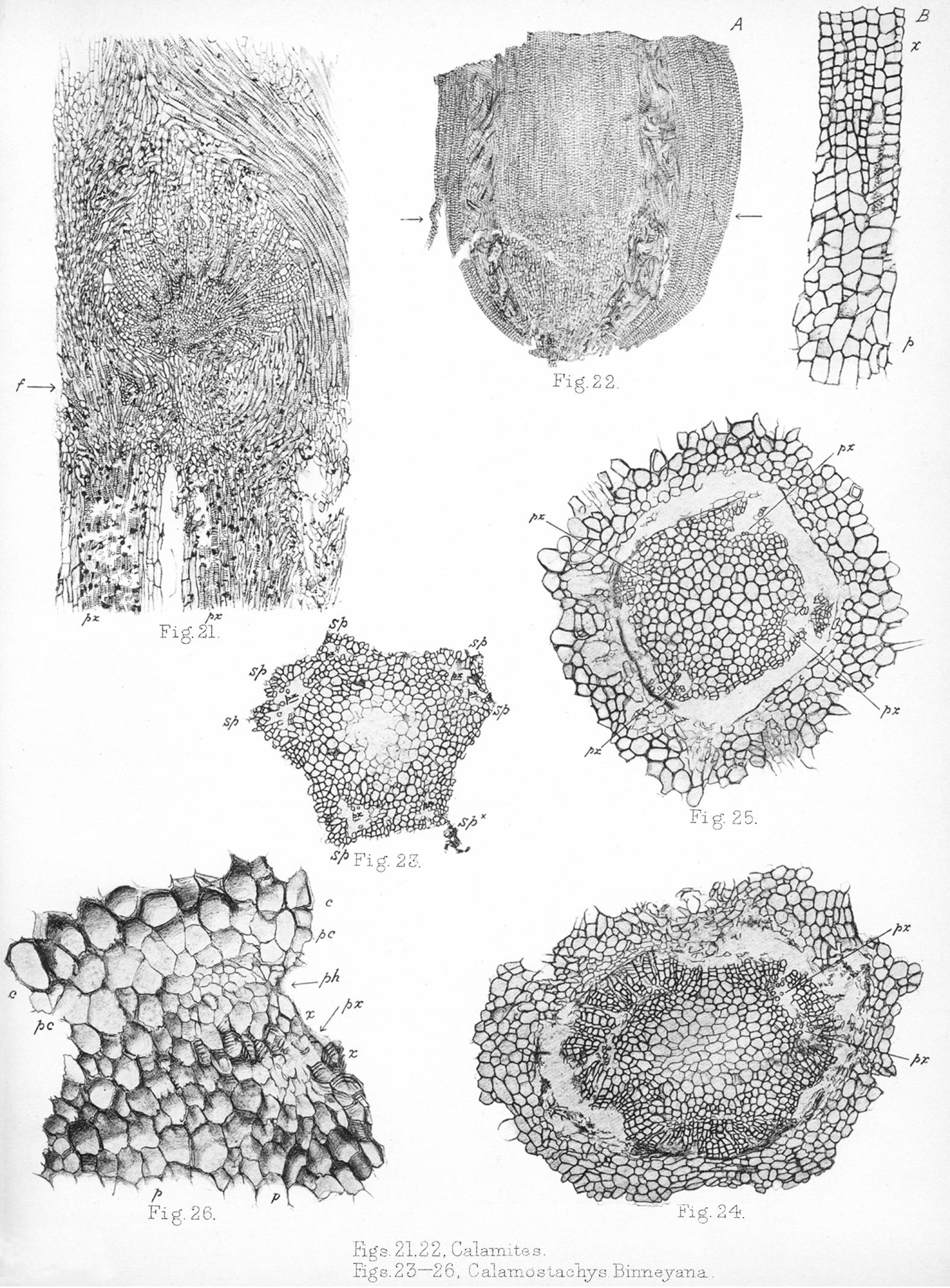


PLATE 80.

Figs. 21 and 22. *Calamites.*

Fig. 21. Part of a tangential section, passing through the primary wood, and showing the base of a branch. Near the bottom of the figure the section has touched on the canals of two bundles, and shows their disorganized protoxylem (*px.*). All the tracheæ have tangential pits—characteristic of the inner wood. In the direction of the arrow (*f*), a foliar bundle is shown. In the same straight line, further to the right, is another group of cells, which represents a similar bundle at the point when it begins to curve outwards. The branch has a minute pith, surrounded by groups of primary xylem. The connection of the latter with the nodal wood of the stem can be clearly seen at the lower side of the branch Secondary wood has only been formed towards the upper side of the branch. The connection with the wood of the stem is entirely from below. From a slide (No. 53) prepared by Mr. LOMAX, in the possession of D. H. SCOTT. × 30.

Fig. 22. *A*. Part of a transverse section of a very large stem, showing in median section, the base of an occluded branch. The pith of the main stem is below the figure. In the branch the pith tapers towards the base. The connection of the wood of branch and stem is shown. Midway between the inner and outer limits of the wood of the stem, at the level indicated by the arrows, the pith of the branch comes to a sudden end, and is replaced by secondary wood seen in transverse section. × 6.

B. Portion of same enlarged, showing transition from pith of branch (*p*) to anomalous wood (*x*) in region indicated by the arrows in *A*. × 70. C.N. 134*.

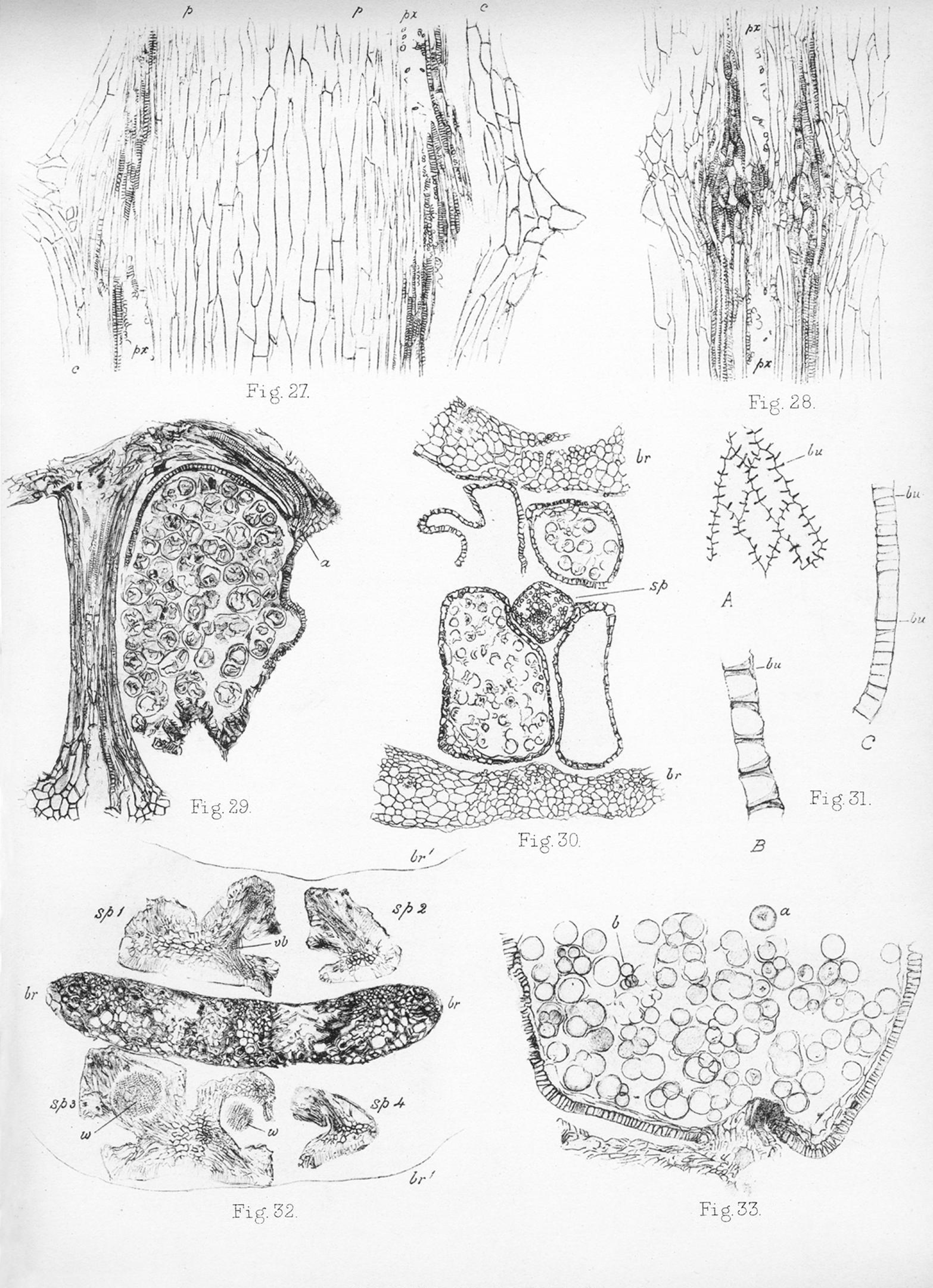
Figs. 23–26. *Calamostachys Binneyana.*

Fig. 23. From a transverse section of a strobilus, showing the central cylinder or stele of the axis. The section passed through a fertile node, bearing 7 sporangiophores. The stele is obtusely triquetrous, with the vascular bundles at its prominent corners. There appear to have been 7 bundles in all; the projecting points of the xylem (*sp*) mark the places where the bundles passing out to the sporangiophores were given off. One such bundle is partly preserved (sp^+). On the inner side of the bundles in the cylinder are irregular canals, in which remains of the protoxylem (*px*) can be traced. All the tissue within the ring of bundles is pith. A few tangential interfascicular cell-divisions have taken place. C.N. 991. × 70.

Fig. 24. From a transverse section of another strobilus, showing the stele and part of the cortex. Here there are probably 6 bundles, in groups of 2 (as at *px*, where their protoxylem is shown). Secondary thickening has made considerable progress. In other respects the structure is similar to that in the last figure. C.N. 1016. × 70.

Fig. 25. From a transverse section of a strobilus, showing the quadrangular stele and part of the cortex. There are 4 vascular bundles, one at each corner. Tangential divisions have begun in the cells of the interfascicular tissue. *px*, the 4 groups of protoxylem. C.N. 1013A. × 70. Compare Plate 74, photograph 14.

Fig. 26. Part of a somewhat oblique transverse section, showing a vascular bundle in connection with the cortical tissues. *p,p*, pith; *x,x*, xylem; *px*, protoxylem; *ph*, phloëm-group; *pc,pc*, probable pericycle; *c,c*, cortex. C.N. 1013. × 200.



Figs. 27—33, Calamostachys Binneyana.

PLATE 81.

Calamostachys Binneyana.

Fig. 27. Part of an approximately median longitudinal section of the axis of a large strobilus. *p,p*, the wide pith of the cylinder; on either side is the xylem of a vascular bundle. Two canals are shown with remains of the protoxylem (*px*), (*px*). *c,c*, the cortex, of which only the inner layers are shown. The section passes through a whorl of sporangiophores. C.N. 1022A. × 70.

Fig. 28. Tangential section through a vascular bundle of the same strobilus. The section passes through a node bearing a whorl of bracts (the second sterile node from below, shown in photograph 10, on Plate 73). The canal of the bundle, with the protoxylem (*px*), is shown both above and below the node. The nodal wood has short reticulated tracheides. In the internode the tracheæ are generally scalariform. The parenchyma on either side belongs to the stele. C.N. 1022. × 70.

Figs. 27 and 28 are from the same preparations as photographs 10 and 11, on Plate 73. Fig. 27 is from a part not shown in the photographs.

Fig. 29. Peltate sporangiophore, with a sporangium attached, from an approximately transverse section of a strobilus. The vascular bundle is shown in the axis of the sporangiophore, and a branch-bundle is seen passing through the peltate expansion, to the base of the sporangium. The sporangium is attached to the edge of the peltate scale, at *a*. Within the sporangium are numerous spore-tetrads, enclosed in their mother-cell membranes. C.N. 996. × 70.

Fig. 30. Part of a tangential section of a strobilus, showing a sporangiophore-pedicel (*sp*) in transverse section, surrounded by its 4 sporangia. The vascular bundle of the sporangiophore is seen. Parts of the adjacent whorls of coherent bracts, *br*, *br*, are shown. Three vascular bundles are shown in the lower, and two in the upper whorl. C.N. 1023. × 50.

Fig. 31. Details of sporangium-wall,

A. In surface view; "buttresses" seen (as at *bu*) projecting from cell-walls into interior of cells;

B. In transverse section of sporangium (tangential of strobilus). Here the "buttresses" (*bu*) are seen from the side, with the thin cell-wall between them. Such a section cuts *across* the cells shown in A.

C. In longitudinal section of sporangium (transverse or radial of strobilus). Here the narrow edges of the "buttresses" (*bu*) are shown. Such a section cuts the cells shown in *A lengthwise*. The difference in the thickness of the wall in *B* and *C* is accidental. C.N. 1003. × 200.

Fig. 32. Part of a tangential section, passing through the peltate expansions of the sporangiophores (*sp*), 4 of which are shown, and also part of the whorl of bracts (*br*) between them. In *sp*. 1 the right-hand dichotomy of the vascular bundle (*vb*) is well shown. In *sp*. 2 the section shows one bundle in transverse section, and a branch-bundle cut longitudinally. In *sp*. 3 parts of the vascular bundles are shown. At two points the section passes through the concavities of the under surface of the scale, and shows part of the wall of 2 sporangia, *w.*, *w.*; *br′.*, *br′.*, outline of adjacent bracts. C.N. 1898A. × 30.

Fig. 33. Part of a sporangium containing spore-tetrads. The extremely unequal size of the different spores of the same tetrad is the point specially illustrated. In many cases (as at *b*) certain spores appear to be quite abortive. At *a*, a mature spore is shown, with the 3 radiating fissures in its membrane. C.N. 1007. × 100.

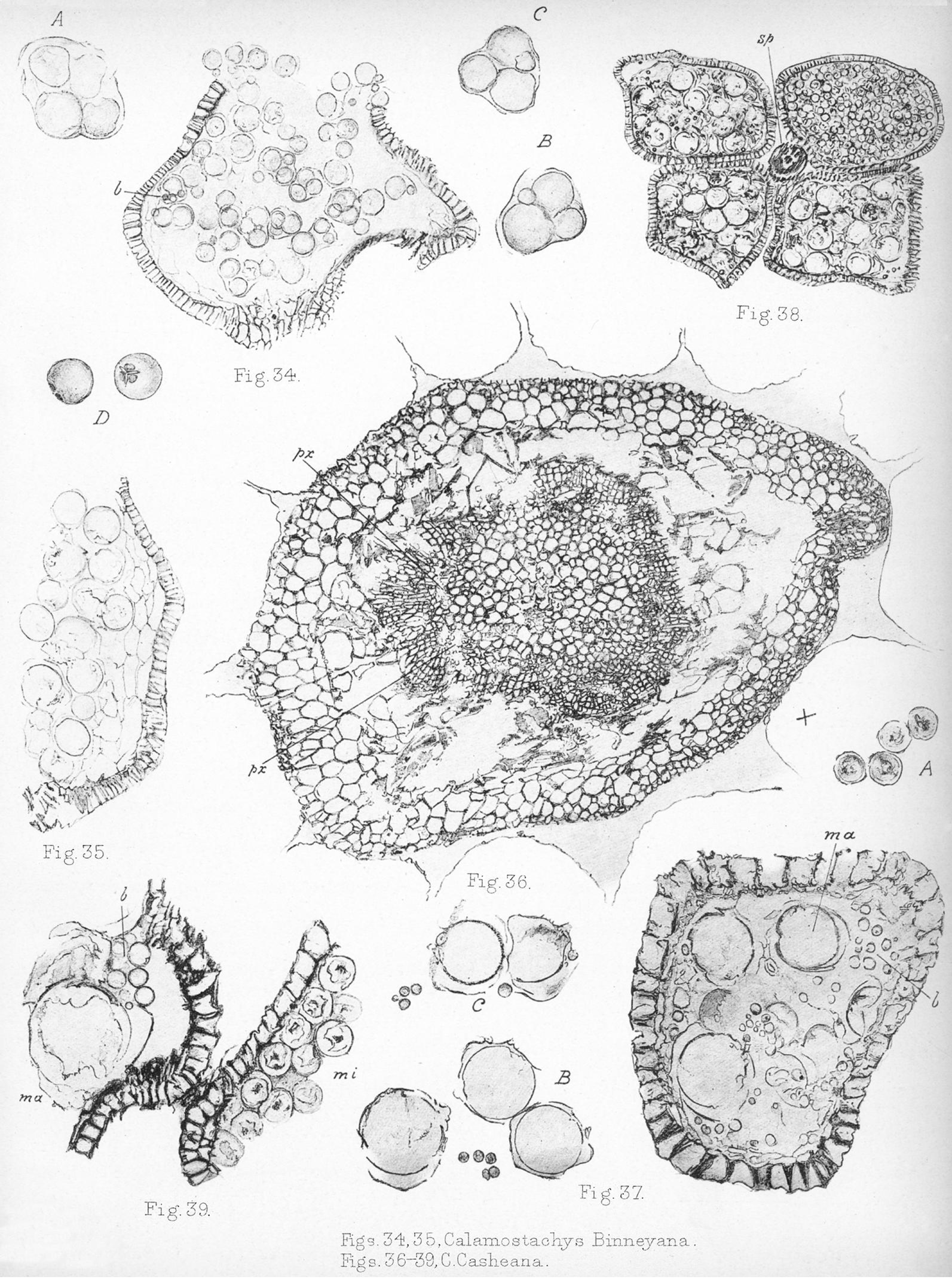


PLATE 82.

Figs. 34 and 35. *Calamostachys Binneyana.*

Fig. 34. Part of a sporangium containing spore-tetrads, to show abortive spores with normal sister-cells. In a tetrad towards the left-hand, 3 out of the 4 spores are abortive (*b*). C.N. 1011. × 100.

A, B, C, and *D*. Tetrads and spores more highly magnified.

A. A normal tetrad. All 4 spores are about equally developed. C.N. 1005. × 200.

B. A tetrad in which one spore is abortive. C.N. 1013A. × 200.

C. A tetrad with one abortive spore, and one of intermediate size. C.N. 1011. × 200.

D. Two mature spores to show fissures and thickening of the spore-membrane. C.N. 1007. × 200.

Fig. 35. Part of a sporangium, to show layer of parenchyma lining the sporangial wall. Within this are mature spores. C.N. 1008. × 150.

Figs. 36–39. *Calamostachys Casheana.*

Fig. 36. Transverse section of the axis of the strobilus. In the middle is the central cylinder, with a large pith, surrounded by 6 vascular bundles. The structure is the same as in fig. 24 (Plate 80), from *C. Binneyana* (*px.*, two of the protoxylem-groups). There is a well-marked zone of radially arranged secondary xylem. Outside this are remains of thin-walled cells, and surrounding the whole is the well-preserved outer cortex. The outlines to the exterior mark the position of the sporangia. This is from the same preparation as photograph 16, on Plate 74. C.N. 1588. × 70.

Fig. 37. Section of a macrosporangium (that marked × in fig. 36), containing several macrospores (as at *ma*), and a large number of abortive spores (as at *b*). There are slight remains of tissue lining the sporangial wall. C.N. 1588.

A. Microspores from the tangential section of the same specimen. C.N. 1587.

B. Macrospores and abortive spores. C.N. 1587.

C. „ „ „ C.N. 1588.

All the above × 100.

Fig. 38. Group of four sporangia from a tangential section, with the pedicel of their sporangiophore (*sp.*) between them. One is a microsporangium; the other three are macrosporangia. Among the macrospores abortive spores are seen. Also shown in Plate 74, photograph 15. C.N. 1587. × 30.

Fig. 39. Parts of two adjacent sporangia from a tangential section of the other specimen of this species. To the right is a microsporangium, containing microspores (*mi*) only. To the left is a macrosporangium, in which one of the macrospores (*ma*) and several abortive spores (*b*) are shown. C.N. 1025. × 100.

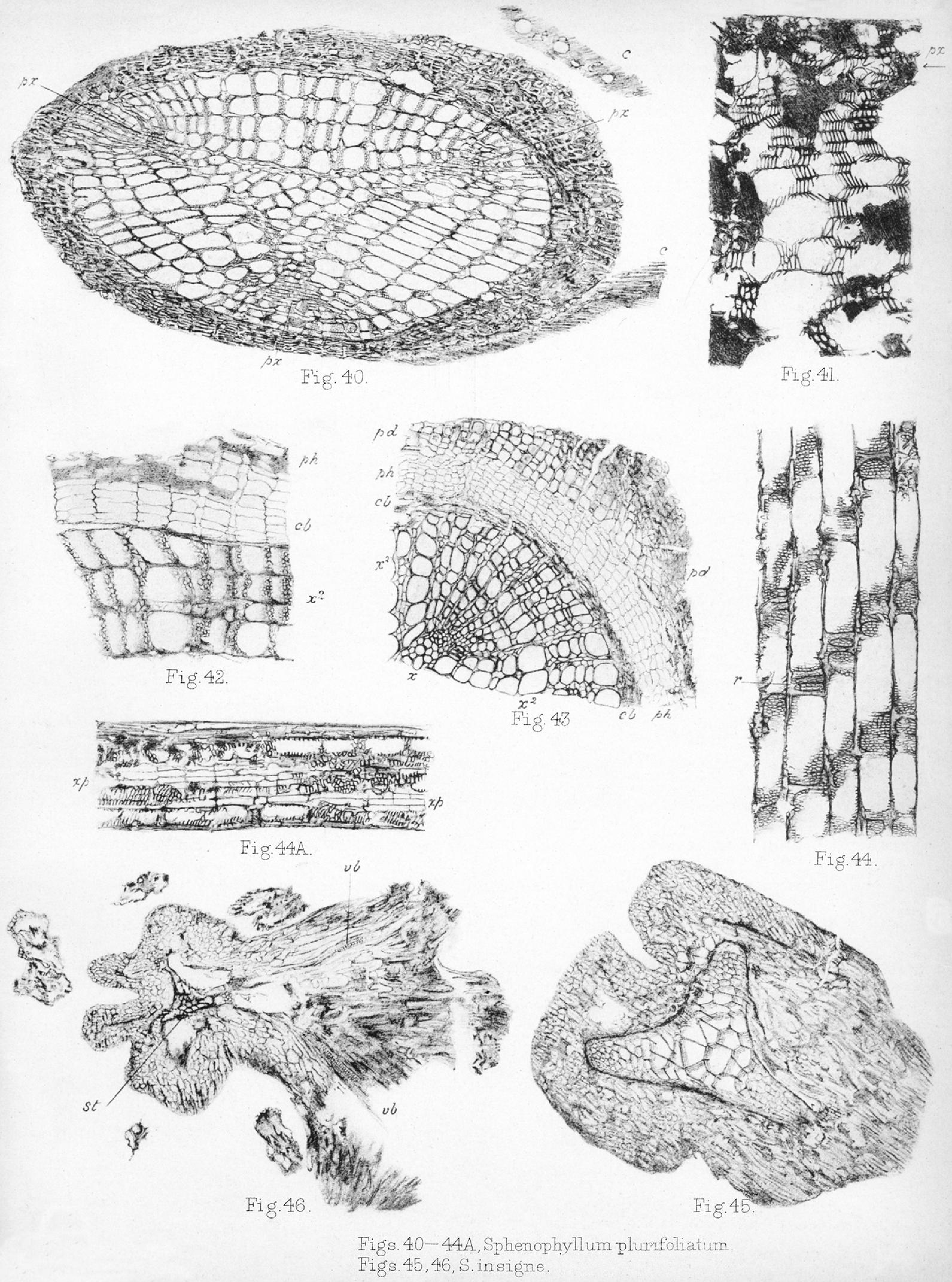


PLATE 83.

Figs. 40–44A. *Sphenophyllum plurifoliatum.*

Fig. 40. Obliquely transverse section of a moderately young stem. In the middle is the triarch primary xylem. The three protoxylem groups at the angles (*px.*), with their small, spiral or reticulated tracheæ, are clearly seen. The more central primary tracheæ are pitted. About four layers of secondary wood have been formed. The parenchymatous cells at the corners of the tracheæ are shown. The wood is surrounded by secondary cortical tissues, probably including both phloëm and periderm. At *c*, *c*, remains of the primary cortex are present, but only a part of this has been drawn. C.N. 897. × 30.

Fig. 41. Part of an oblique section, showing a portion of the primary xylem. In the direction of the arrow (*px*) is a group of protoxylem, with spiral tracheæ, partly uncoiled. Adjoining these below are scalariform tracheæ, and below these again are pitted elements. Above the protoxylem a small portion of the secondary wood is indicated. C.N. 893. × 200.

Fig. 42. Part of an approximately transverse section, to show secondary wood, x^2; cambium, *cb*; and phloëm, *ph*. C.N. 882. × 70.

Fig. 43. Part of a transverse section (the same as that shown in photograph 19 on Plate 75); *x*, part of primary xylem; x^2, secondary xylem; *cb*, cambium; *ph*, phloëm; *pd*, internal periderm. C.N. 894. × 50.

Fig. 44. Part of a radial section through the secondary wood, showing the *radially-elongated* parenchymatous cells (as at *r*), passing between the tracheæ. C.N. 884. × 50.

Fig. 44A. Part of another, approximately radial section, showing the longitudinal strands of xylem-parenchyma, *x.p.*, *x.p.*, and portions of the radial cells connecting them. C.N. 903. × 50.

Figs. 45 and 46. *Sphenophyllum insigne.*

Fig. 45. Approximately transverse section of a young stem, without any secondary thickening. In the middle is the triarch primary xylem, with protoxylem at the three angles. Surrounding this are the primary cortical tissues. C.N. 911. × 50.

Fig. 46. Transverse section of a very young stem, showing part of a whorl of coherent leaves, in which two foliar vascular bundles are seen (*v.b.*). The fragments of tissue seen to the exterior are probably portions of leaves. *st* = stele of stem. C.N. 917. × 50.

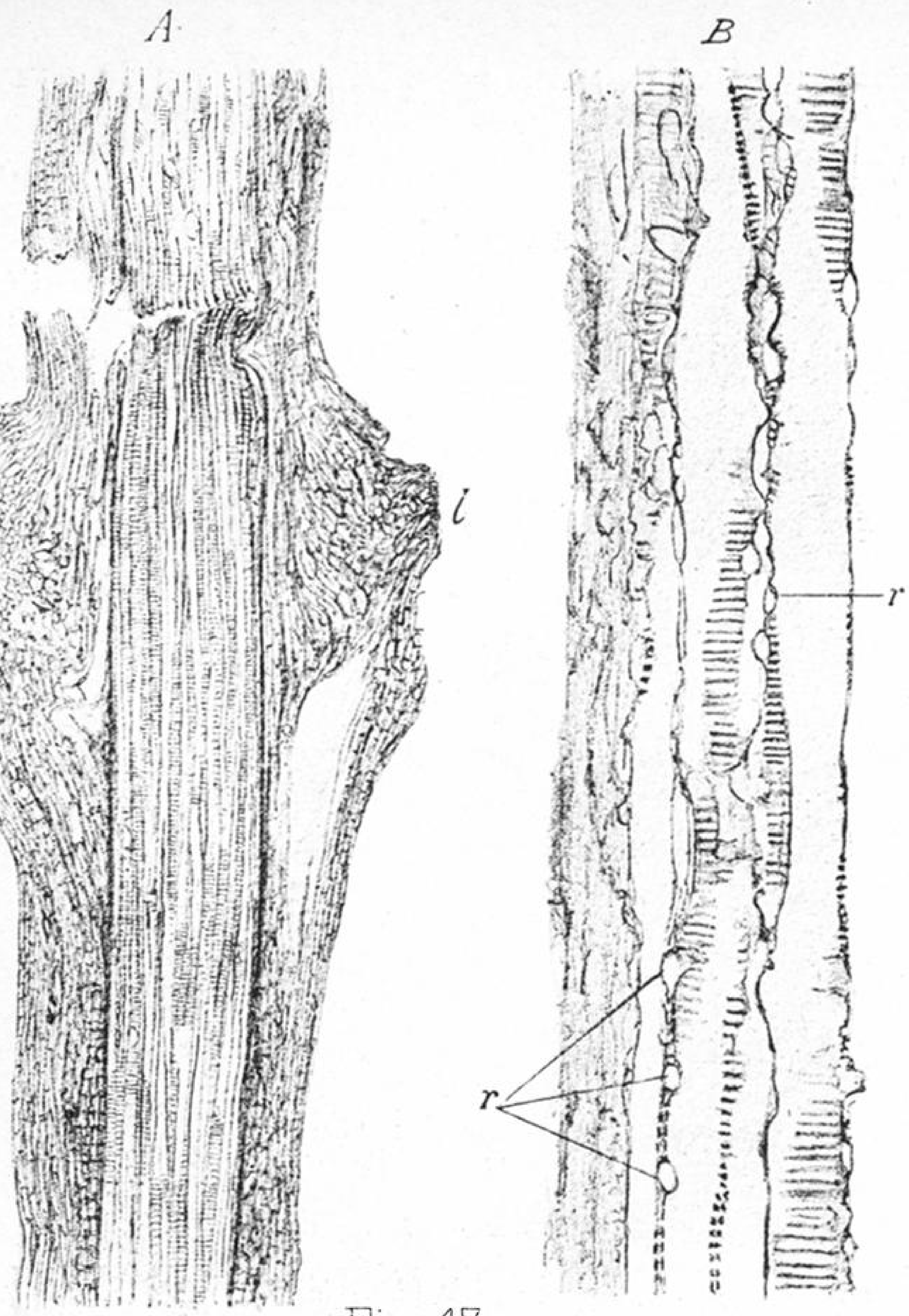


Fig. 47.

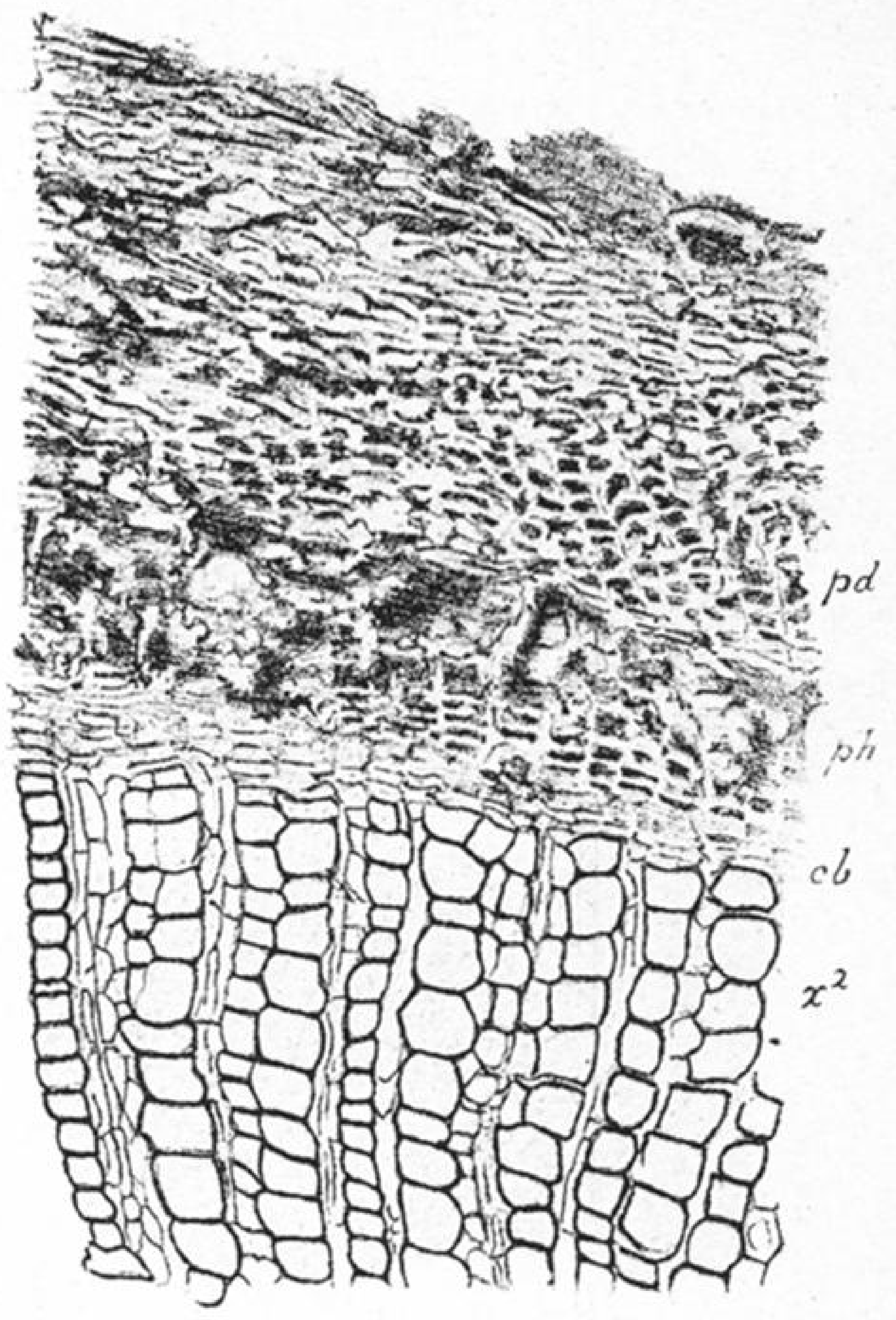


Fig. 48.

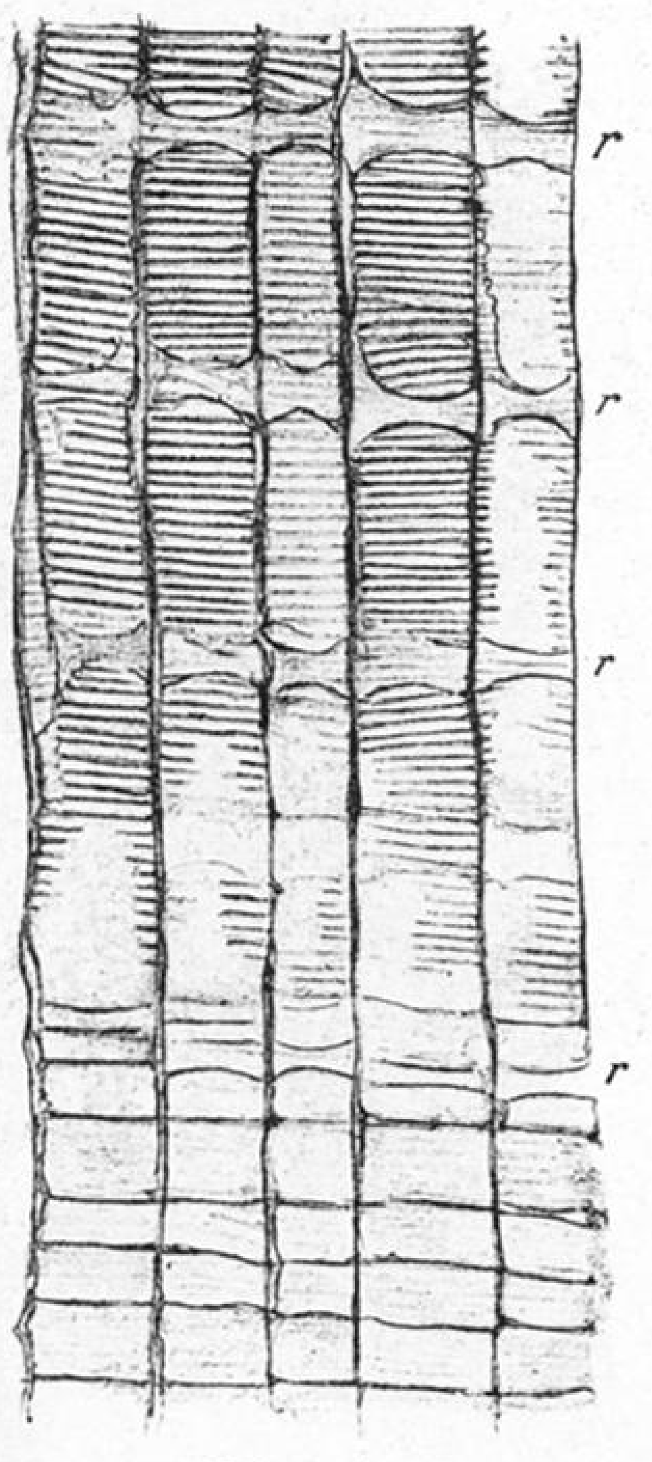


Fig. 49.

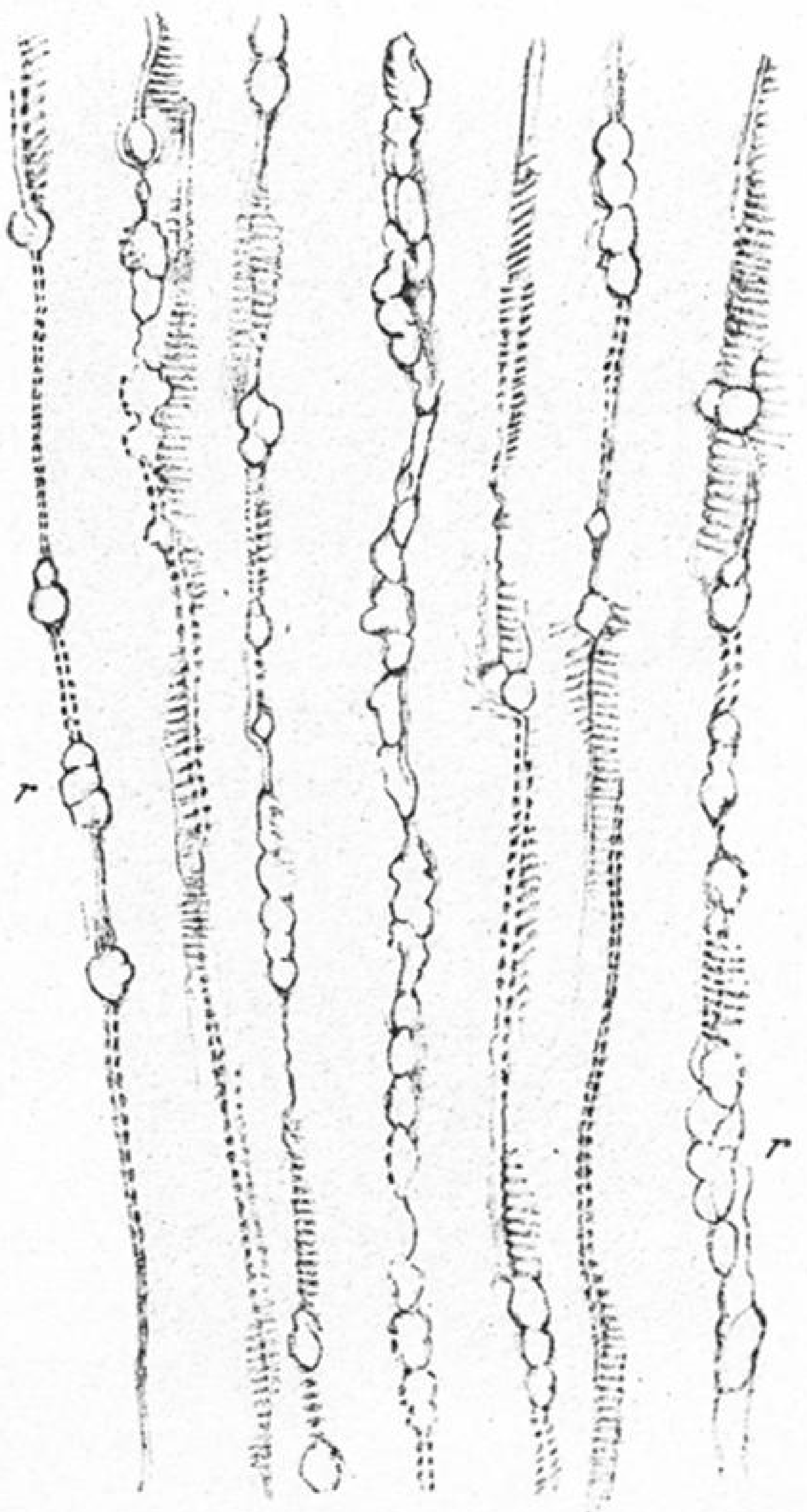


Fig. 50.

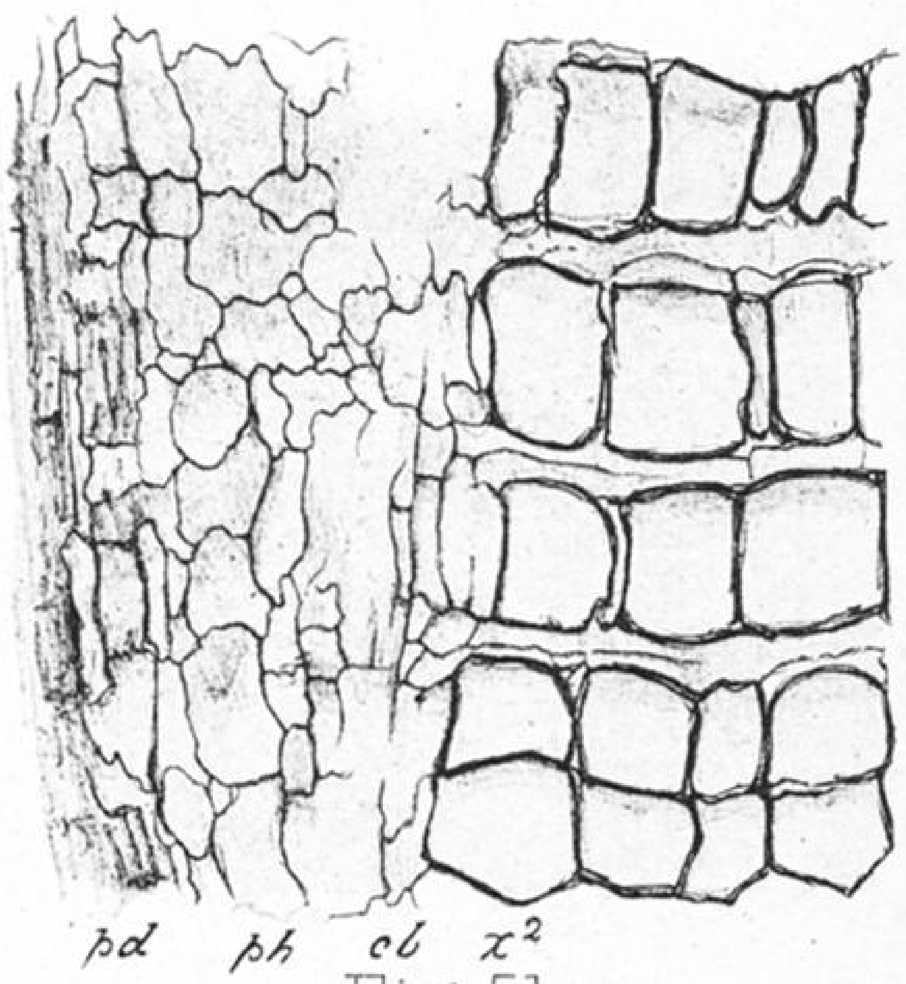


Fig. 51.

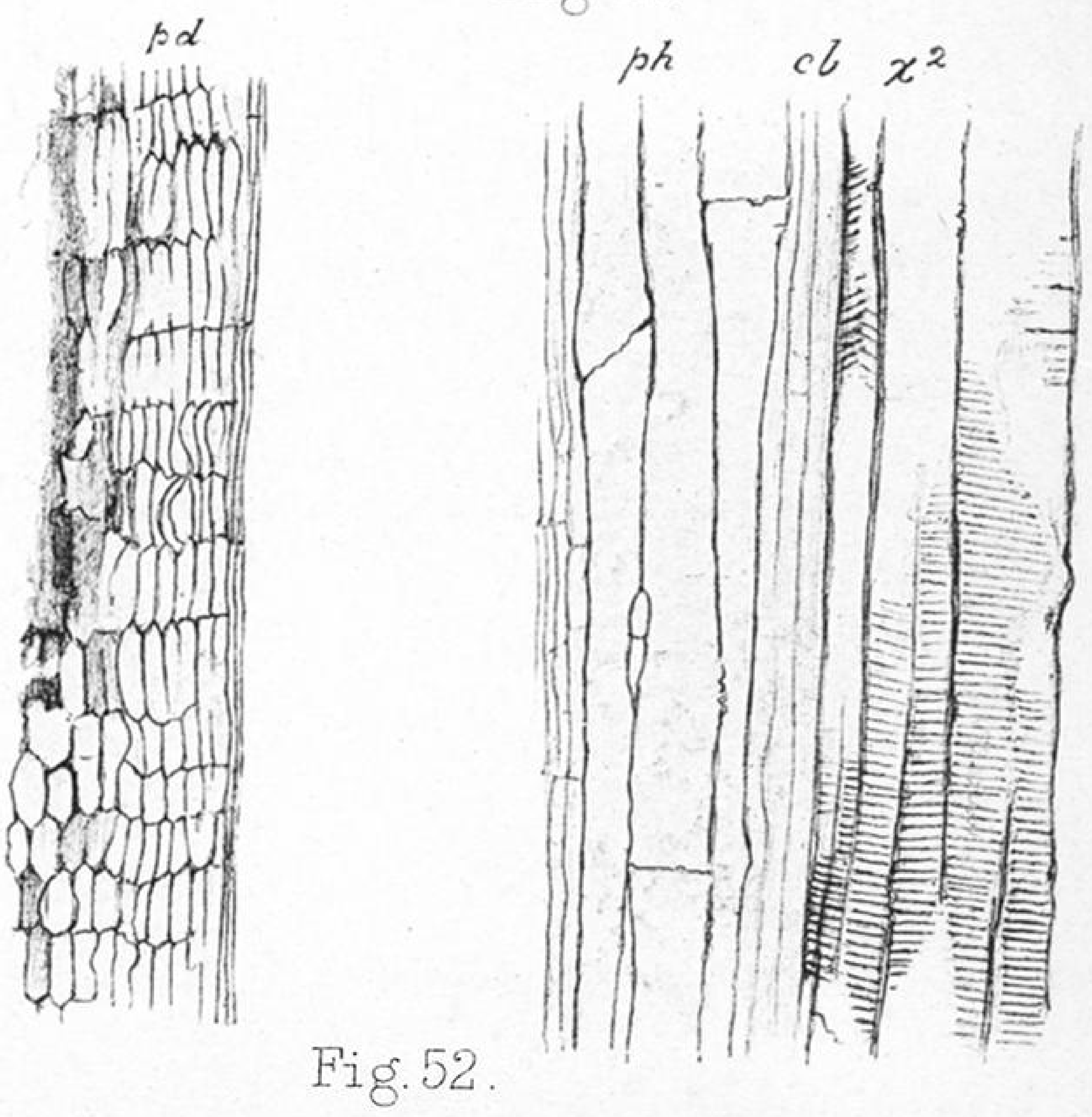


Fig. 52.

Figs. 47—52, Sphenophyllum insigne.

PLATE 84.

Sphenophyllum insigne.

Fig. 47. *A.* Longitudinal median section, passing through a node. *l, l,* bases of leaves. × 13.

B. Portion of wood from the same preparation, seen in tangential, but somewhat oblique section. The scalariform markings of the tracheæ, and the medullary rays (r) are seen. *Cf.* fig. 50. C.N. 1420. × 100.

Fig. 48. Part of the transverse section of the largest stem, showing secondary wood, x^2; cambium, *cb*; phloëm, *ph*; and internal periderm, *pd*. C.N. 914. × 50.

Fig. 49. Part of the secondary wood of the same specimen, in radial section; r, medullary rays. C.N. 924. × 100.

Fig. 50. Part of the secondary wood of a large stem, in tangential section, showing the medullary rays (r), of various heights, and the scalariform pits of the tracheæ; compare with fig. 47B. C.N. 921. × 100.

Fig. 51. Part of a transverse section of the largest stem. x^2, secondary wood; *cb*, cambium; *ph*, phloëm; *pd*, inner layers of periderm. C.N. 913. × 100.

Fig. 52. Corresponding radial section from the same specimen; lettering as before. Note the elements in the phloëm resembling sieve-tubes.

The separation between periderm and phloëm is accidental; in other parts of the section they are continuous. The delicate layer which is severed is probably phellogen. C.N. 924. × 100.

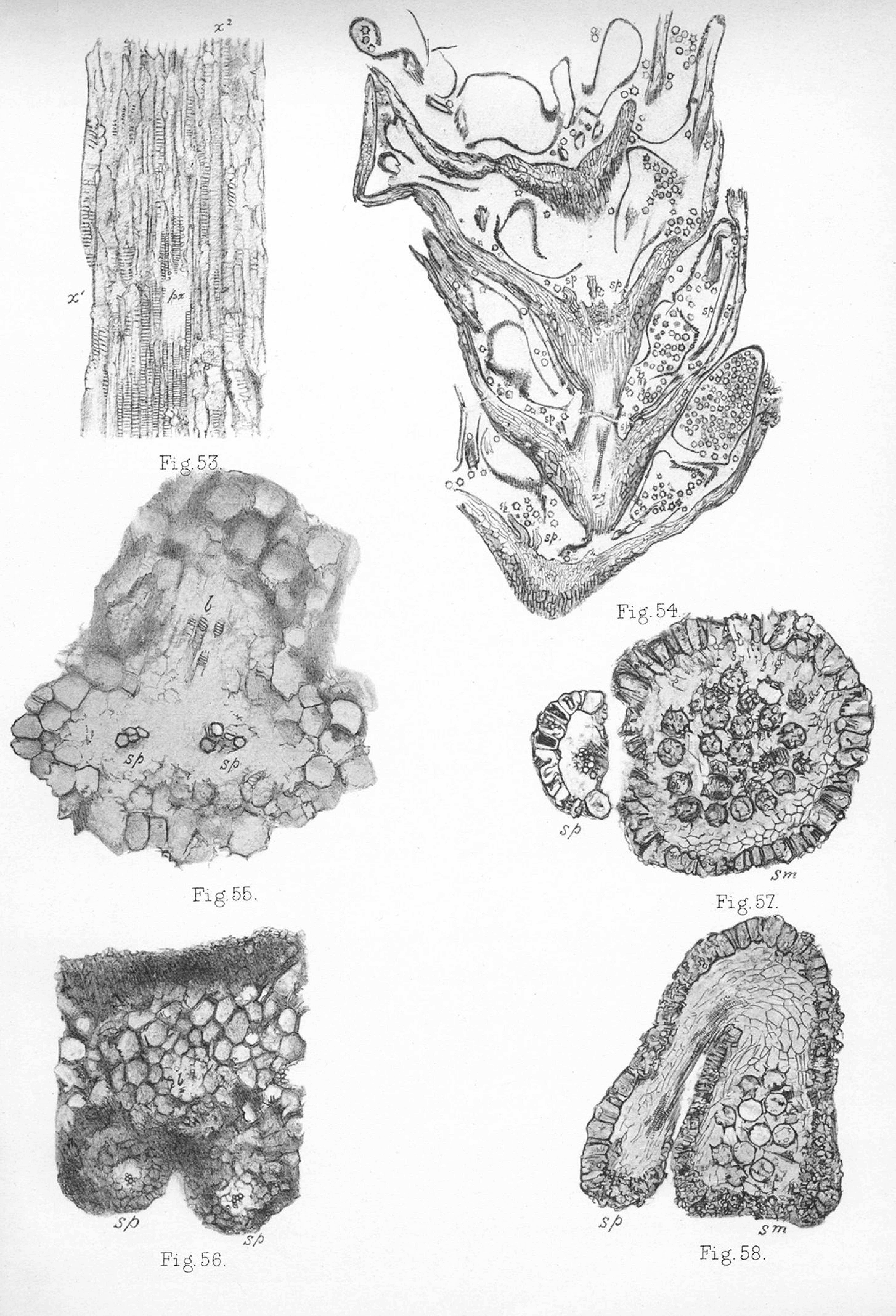


Fig.53, Sphenophyllum insigne.
Figs.54–58, S. Dawsoni.

PLATE 85.

Fig. 53. *Sphenophyllum insigne.* Part of a longitudinal section of the wood, passing through the canal, and showing the spiral tracheæ of the protoxylem, *px.* To the left of the canal is primary xylem, *x*; to the right the secondary wood, x^2, begins. The section is somewhat oblique.

From a stem of moderate size, with secondary wood 7–9 cells thick. C.N. 922. × 100.

Figs. 54–58. *Sphenophyllum Dawsoni.*

Fig. 54. Part of a longitudinal section of a small strobilus, showing 4 whorls of bracts. The section is partly radial, partly tangential. *x*, part of xylem of axis; *sp*, various sporangiophores, showing attachment to bracts. Fragments of sporangia, and numerous spores, are shown. C.N. 1898K. × 15.

Fig. 55. Part of a transverse section, through the whorl of bracts close to its insertion on the axis. From the section figured by Williamson, "Organization," Part XVIII., Plate 27, fig. 9. Three bundles are shown just separating from one another. *b.*, bundle going to a bract; *sp*, *sp*, bundles going to two sporangiophores. C.N. 1049A. × 200.

Fig. 56. Corresponding section from the same specimen, taken through the whorl of bracts, a little higher up than the last. From the section figured by Williamson, *loc. cit.*, Part XVIII., Plate 26, fig. 2. The three bundles have now quite separated, and the projecting bases of the sporangiophores are seen. *b*, bundle going to bract; *sp*, *sp*, bases of sporangiophores. C.N. 1049B. × 100.

Fig. 57. Transverse section through a sporangium, *sm*, and its sporangiophore, *sp*. In the former, delicate tissue lining the wall is shown, and within this the spores. In the sporangiophore, the xylem of the vascular bundle is evident. C.N. 1898H. × 60.

Fig. 58. Corresponding longitudinal section of a sporangium and part of its sporangiophore, showing the attachment. The vascular bundle of the sporangiophore is shown. The section is somewhat oblique. C.N. 1898E. × 60.

PLATE 86.

This contains figures, from photographs, of medullary casts of *Calamites*. For description, see text, pp. 896–899.

All the figures are much reduced. F is rather more than a quarter of natural size; all the rest are rather more than half natural size.